4. *The Skull of* Tapinocephalus *and its near Relatives.* By Lieuwe Dirk Boonstra. (With Plate IV and seventeen text-figures.)

Introduction

All the known cranial material of the South African Tapinocephalidae is to be considered in this communication. I have examined the specimens in the British and American Museums of Natural History and those housed in the South African Museum. Adequate material exists of the genera *Tapinocephalus*, *Mormosaurus*, *Keratocephalus* and *Phocosaurus*, whereas of *Taurops* there is only a snout and of *Pelosuchus* only a single weathered dentary.

Historical

In 1876 Owen[13] made a snout the type of *Tapinocephalus atherstonei* and, although a part of the occiput and a part of the supraorbital region were associated, they were not described or figured.

Seeley in 1888[14] founded *Phocosaurus megischion* on a pelvis and this specimen with other associated bones were included by Lydekker[12] in the genus *Tapinocephalus* until I[4] revived Seeley's name *Phocosaurus*.

Broom's genus *Pelosuchus*,[5] founded on a weathered dentary, includes among other bones a fairly good femur and it was on the structure of these postcranial bones that I[4] recently included this genus in the Tapinocephalidae.

The first good Tapinocephalid skull was described by Broom[6] in 1909, in as Watson terms it 'a . . . somewhat inaccurate account' and referred it to Owen's *Tapinocephalus atherstonei* and subsequently (1914) it was made the type of the genus *Mormosaurus* by Watson.[15]

In the meantime (1912) Broom[7] had created the genus *Taurops* on a very inadequate weathered snout, and in 1913 Haughton[10] had published some poor photographs of a very good skull of *Tapinocephalus* in the South African Museum (No. 2344).

In 1928 Broom[8] described an incomplete skull of *Tapinocephalus*, which I refigured in 1936.[1]

In 1931 von Huene[11] founded the genus *Keratocephalus* on some pieces of a skull associated with some postcranial bones, and in 1951 I[2] figured an imperfect skull in the South African Museum which I referred to the same genus.

In 1936 I[1] arranged the then known genera of the South African Tapinocephalia into a number of groups in an attempt to facilitate our study of the various described forms. In this admittedly arrangement of convenience I grouped *Taurops* and *Keratocephalus* with *Tapinocephalus*, and included *Mormo-*

saurus in another group containing *Taurocephalus* and *Struthiocephalus*. Recently, in a study of the girdles and limbs, I[4] have included in the former group *Pelosuchus* and *Phocosaurus* and am here also transferring to it Watson's *Mormosaurus*.

In the Tapinocephalidae, thus including the genera *Tapinocephalus*, *Phocosaurus*, *Mormosaurus*, *Taurops*, *Keratocephalus* and *Pelosuchus*, the structure of the skull, considered as a group, can be described as follows:

The General Shape and Form of the Skull

The Tapinocephalid skull is large and massive (length 516–600 mm., width 456–543 mm., height 315–384 mm.). The snout is relatively weak, short, low to fairly low and fairly wide to wide (preorbital length 273–330 mm., height 144–186 mm., width 222–330 mm.).

The orbit, which is relatively small, lies wholly in the posterior half of the skull. The bones of the preorbital half of the skull are relatively unthickened, whereas the posterior half has the bones, particularly of the roof, greatly pachyostosed. In the latter the surface is rough, whereas in the former it is smooth. In this group the thickening also affects the 'cheek', whereas in *Struthiocephalus* and its allies this remains relatively unthickened and the surface is smooth. The pachyostosis of the dorsal cranial bones is accentuated in centres in *Keratocephalus* (*vide Struthiocephalus*), whereas in the other genera these centres coalesce, so that in the former the distinct naso-frontal boss and a parietal mound are present, whereas in the other genera these are incorporated in the general pachyostosis. This pachyostosis extends furthest anteriorly in *Tapinocephalus* and extends less anteriorly in *Phocosaurus*, *Mormosaurus* and *Keratocephalus* in this order. There is a distinct and abrupt step from the facial to the cranial surface. The postorbital bar is greatly thickened and massive, but its postfrontal part is not boss-like, but has its surface flowing evenly into the general thickening of the upper cranial surface.

The orbits are of moderate size and look forwards and outwards, posteriorly bounded by the massive outwardly thickened postorbital bar, dorsally overhung by the thick pre- and postfrontals; anteriorly the border is much less thickened, except in *Tapinocephalus* where the dorso-anterior part is also thickened.

The nostrils are fairly large and oval, situated on the dorsal surface and directed mainly dorsally and but little laterally; they lie well back from the anterior tip of the snout and are separated from each other by a strong internarial bar.

The temporal fossa is slitlike in all but *Keratocephalus*, where the antero-posterior diameter is not so reduced; dorsally the bay, characteristic of most species of *Struthiocephalus*, is obliterated in all except *Keratocephalus*, where remains of a bay are still apparent.

The interparietal width is fairly to very large (120–240 mm.) with only a slight pinching-in to form a bay in *Keratocephalus*.

Due to the forward position of the quadrate the lower jaw is short and the gape of the jaws fairly small.

In dorsal view the occipital edge is nearly straight except in *Tapinocephalus* where it is concave.

The Bones of the Dorsal and Lateral Surfaces

The premaxillaries (P.M.) form the upper median surface of the snout, stretching from the anterior border posteriorly nearly to or beyond the plane of the antorbital border. The posterior extent is least in *Tapinocephalus* and *Keratocephalus* and most in *Phocosaurus* and *Mormosaurus*. The premaxillaries form a strong internarial bar and then taper in posterior direction—becoming very narrow in *Phocosaurus* and *Mormosaurus*—to lie in a grove in the nasals. The abrupt step from snout to cranial roof causes the posterior part of the premaxillaries to be sharply turned up in *Tapinocephalus*, but less sharply in *Keratocephalus*, *Mormosaurus* and *Phocosaurus* in this order.

The nasals (N.) are a pair of long, narrow bones tapering somewhat anteriorly; anteriorly separated by the premaxillaries and posteriorly forming a groove to receive the posterior ends of the paired premaxillaries; posterior to the limits of the premaxillaries the nasals meet in the median line and are here greatly to very greatly thickened to form the antero-median part of the pachyostosis of the cranial roof and the greater part of the distinct naso-frontal boss of *Keratocephalus*; at the line of thickening the surface of the nasal is bent more or less sharply upwards, thus facing more or less anteriorly; here each nasal carries a depression presumably to house some facial gland. In all but *Keratocephalus* the nasal thickening is confluent with that of the prefrontal, but in *Keratocephalus* these two thickenings are separated by a shallow groove.

The septomaxillaries (S.M.) are small bones forming the lower border and floor of the nostrils and extend posteriorly as narrow tapering splints between the nasal and maxilla.

The maxillaries (M.) are the largest bones of the snout, being long but low; posteriorly a dorsal prong meets the prefrontal, and a ventral prong extends further posteriorly with its upper edge meeting the ventro-anterior edge of the jugal. In the indentation between these two prongs lie the anterior ends of the jugal and the lacrimal. The ventral edge of the maxilla is fairly straight and this straight edge curves very slightly upwards anteriorly, where it is continued by the lower edge of the premaxilla.

The lacrimal (L.) is a small, low and relatively short bone. It is shortest in *Tapinocephalus*, somewhat larger in *Mormosaurus* and *Phocosaurus* and unknown in *Keratocephalus*. It forms only a small part of the median part of the anterior orbital border, which is relatively unthickened. It is overhung by the prefrontal—greatly so in *Tapinocephalus*, but much less in the other genera, where the anterior part of the prefrontal is not greatly swollen. It has no contact with the nasal, because of the intercalation of the dorsal prong of the maxilla.

The jugal (J.) is a strong bone; like the bones of the snout it is not greatly thickened and its surface is smooth, being without pits and rugae. It forms the antero-ventral, relatively unthickened, border of the orbit. It extends far ventrally, decreasing in width, with its anterior edge curving down sharply from the contact with the maxilla. Its ventral edge meets the quadratojugal in a firm suture in all the genera except *Mormosaurus*, where there is a deep incisure reminiscent of that shown in *Struthiocephalus*. Its anterior prong is short in *Tapinocephalus*, somewhat longer in *Mormosaurus* and long and high in *Phocosaurus*. Its posterior edge presents a shallow curve, where it meets the anterior wedge-like prolongation of the squamosal; this indentation is deepest in *Mormosaurus* and shallowest in *Tapinocephalus*.

The prefrontal (Pr. F.) is very greatly thickened along its lateral border to form the very thick rugose overhanging antero-dorsal border of the orbit. In *Tapinocephalus* it is swollen right up to its antero-ventral edge and thus strongly overhangs the lacrimal but in the other genera its anterior quarter is relatively unthickened. In all the Tapinocephalid genera it meets the maxilla, and the lacrimal is thus excluded from contact with the nasal. In dorsal view its width is seen to vary, this also in specimens of the same genus. Posteriorly it meets the postfrontal so that the frontal is excluded from the orbital border, but a longer or shorter tongue of the frontal represents the original participation of the frontal in the orbital border before the overgrowing swelling of the prefrontal and postfrontal pushed it out. Medially the swelling of the prefrontal is confluent with that of the nasal and frontal in all except in *Keratocephalus*. Here the prefrontal is medially thinner and a shallow groove-like hollow clearly demarcates it from the naso-frontal boss, as is also the case in the genus *Struthiocephalus*. An anterior tongue of the frontal is intercalated between the nasal and the prefrontal for a considerable distance in *Keratocephalus* but less in the other genera and least in *Tapinocephalus*.

The frontal (F.) is the largest bone of the dorsal skull roof. Its median part is roughly rectangular and from this body three tongues diverge; the posterior tongue is the strongest and extends as a fairly thin to fairly wide wedge, lying between the postfrontal and parietal to enter the border of the temporal fossa in its antero-dorsal part; the anterior tongue, already mentioned as a fairly narrow tapering wedge separating the posterior part of the nasal from the prefrontal, is much weaker than the posterior tongue and in *Keratocephalus* lies in the deepest part of the groove, lateral to the frontonasal boss; the lateral tongue is weak and only separates the pre- from the postfrontal for a short distance medially. Anteriorly the frontals are greatly thickened at their junction with the nasals, where, in *Keratocephalus* they form the posterior fifth of the naso-frontal boss, and in the other genera coalesce in the general pachyostosis. Behind the naso-frontal swelling the frontals remain thick and swollen in *Tapinocephalus* and *Phocosaurus*, but in *Mormosaurus* and particularly in *Keratocephalus* are reduced in thickness to form a saddle between the elevated naso-frontal boss and a mound on the parietal. Laterally the frontals are

elevated near their contact with the postfrontals, forming a distinct ridge in *Mormosaurus*, which is reminiscent of a similar condition in *Struthiocephalus akraalensis*. Posteriorly the frontals meet the parietals in a shallowly to deeply curved suture just anterior to the pineal foramen.

The postfrontal (Po. F.) forms the dorso-posterior corner of the orbital border, which is here greatly thickened and rugose, and forming the upper part of the postorbital bar, extends to the margin of the post-temporal fossa. (Its posterior extent is inconstant and it is sometimes excluded from the margin of the temporal fossa by the overgrowing of the postorbital. Even in the same skull this inconstancy is shown, where it reaches the temporal fossa on one side but not on the other.) The postfrontal, although greatly thickened and massive, does not form a distinct boss (as in *Anteosaurus*) because the frontal above and the postorbital below are equally thickened with the swellings coalescing. The great thickening of the postfrontal coalescing with that of the prefrontal overgrows the lateral tongue of the frontal and thus excludes that bone from the orbital border. The postfrontal forms a greater part of the dorso-posterior thick orbital border in *Phocosaurus*, a small part in *Tapinocephalus*, a small or great part in *Keratocephalus* and a moderate part in *Mormosaurus*.

The parietals (P.) as a pair form a much smaller part of the cranial roof than do the two frontals. A moderate to large pineal foramen lies near the frontal suture. The antero-posterior length varies considerably even in the same genus; in *Mormosaurus* and *Phocosaurus* it is very short, moderate in *Tapinocephalus* and moderate to fairly long in *Keratocephalus*. In three of the known *Keratocephalus* specimens the pineal foramen is surrounded by a low moundlike boss, whereas in a fourth this area is flat to depressed. In one specimen of *Tapinocephalus* this area is depressed, whereas in another there is a mound; in *Mormosaurus* there is a low mound and in *Phocosaurus* this area is flat. There is a considerable variation in the intertemporal width of the parietals; the intertemporal width is great in *Tapinocephalus* (240 mm.), fairly great in *Mormosaurus* (201 mm.), moderate in *Phocosaurus* (177 mm.) and moderate to fairly small in *Keratocephalus* (120–158 mm.). In *Keratocephalus* there is still some indication of the pinching in to form a bay to the temporal fossa, as in some species of *Struthiocephalus*; and in one specimen of *Tapinocephalus* there is a narrow niche in the upper part of the temporal fossa. The parietal forms a sharp edge to the upper border of the temporal fossa; from here the parietal presents a lateral more or less vertical face within the temporal fossa and here meets the posterior flange of the postorbital and the dorsal flange of the squamosal. Laterally the parietal enters the posttemporal arch, extending as a thin wedge between the squamosal and the tabular in most of the skulls examined, but in one specimen of *Keratocephalus* the tabular enters the border of the temporal fossa and the parietal does thus not enter between the squamosal and the tabular, at least on the surface. The degree to which this parietal tongue, between the tabular and squamosal, is visible on the surface of the posttemporal arch is dependent on the amount of overgrowth

of the tabular. Posteriorly the parietals are buttressed by the tabulars and interparietal.

The postorbital (P.O.) is a massive bone forming the lower part of the broad and massive postorbital bar; anteriorly it forms the greatly thickened postero-ventral part of the orbital border and posteriorly most of the thickened anterior border of the temporal fossa. Ventrally it abuts against the squamosal in a long curved suture, and anteriorly meets the jugal along a short suture. Dorsally it meets the postfrontal along a curved suture running across the postorbital bar, but posteriorly the postorbital sometimes ascends along the border of the temporal fossa to meet the frontal and thus excludes the postfrontal from the border of the temporal fossa. (This inconstancy is even seen in the same skull, where the postorbital excludes the postfrontal from the margin of the temporal fossa on the one side but not on the other.) Within the temporal fossa the postorbital sends a short flange upwards and backwards to meet the descending face of the parietal and at a lower level it meets the anteriorly directed flange of the squamosal, which lies within the temporal fossa of which it forms most of the posterior lining.

The squamosal (Sq.) is the main constitutent bone of the 'cheek'. It is a strong element, greatly to very greatly thickened. Its outer surface is swollen in *Tapinocephalus*, flat and smooth in *Keratocephalus*, with a strong ridge in *Mormosaurus*, and with a ridge, knobs and hollows in *Phocosaurus*. Anteriorly it meets the jugal in a long curved squamous suture—shallowly indented in *Tapinocephalus* and *Keratocephalus*, but deeply in *Phocosaurus* and very deeply in *Mormosaurus*. In its antero-ventral corner it receives the quadratojugal, which appears to be wedged into it, with a tongue of the squasmosal overlapping the postero-lateral surface of the quadratojugal. Dorsally it is overlapped by the strong postorbital along a long curved suture and furthei posteriorly it forms the thick lower and most of the thick posterior border of the temporal fossa and much of the posttemporal arch. From the edge of the temporal fossa it sweeps inwards to form most of the facing of the anterior surface of the posttemporal arch and here its dorsal edge overlaps the lower part of the lateral face of the parietal and at a lower level meets the postorbital. On the surface of the posttemporal arch the squamosal meets the dorso-lateral tongue-like process of the parietal, which is usually intercalated between the squamosal and the tabular for a longer or shorter distance; but in one specimen of *Keratocephalus* a thickening of the tabular prevents the squamosal from meeting the parietal on the surface of the posttemporal arch. Lower down the posterior face of the squamosal is covered by the tabular. Postero-ventrally the squamosal forms the thickly rounded postero-ventral edge of the skull. This rounded border forms the outer wall of the 'auditory' groove; medially of this groove the squamosal forms a strong and prominent curved ridge which forms the inner wall of the 'auditory' groove.

The tabular (T.) in dorsal view presents only its upper and lateral edge, which forms the postero-lateral corner of the skull, lining the posterior face of

the parietal and the upper part of the upsweeping squamosal. In lateral view the tabular is seen to present its edge, which forms most of the posterior edge of the skull.

The interparietal (I.P.) in dorsal view just shows its upper edge which lines the median part of the posterior parietal edge. Its width from side to side is small in *Tapinocephalus* and *Mormosaurus*, fairly great in *Phocosaurus* and variable in *Keratocephalus*.

The quadratojugal (Q.J.) in lateral view presents a small to moderate surface. It tapers postero-dorsally and this end is firmly wedged into the antero-dorsal surface of the squamosal. It has quite a strong contact with the jugal, except in one specimen of *Mormosaurus*, where there is a notch at the junction of jugal with quadratojugal. The quadratojugal is firmly clasped by the squamosal especially along its posterior edge where the squamosal has a long ventral process.

The quadrate (Q.) in lateral view has only the outer cotylar face exposed antero-ventrally of the limits of the quadratojugal.

The Occiput

The occiput is adequately preserved only in *Tapinocephalus*, fairly well in *Mormosaurus* and poorly in *Phocosaurus* and *Keratocephalus*.

The occiput of the Tapinocephalidae forms a large surface, very much broader than high. It is shallowly concave from side to side. Along its median line the occiput is nearly vertical, with its dorsal edge, however, lying somewhat further posteriorly than its ventral edge. Along the median line the plane of the occiput makes an angle of slightly more than 90° with the plane in which the alveolar borders of the maxillaries lie. In the median line there is a robust ridge on the interparietal which runs to the upper rounded edge of the occiput. On both sides of the median ridge there lies a deep depression—very deep in one specimen (S.A.M. 11294) of *Keratocephalus* and not very deep in *Phocosaurus* (S.A.M. 11997). The upper edge of the occiput is thick and rounded and overhangs the lower part of the occiput.

The condyle is directed postero-ventrally so that the skull would hang downwards. The condyle forms a stout rounded knob that has its dorsal surface excavated by a shallow groove leading into the *foramen magnum*. The dorso-lateral corners of the condyle are formed by the exoccipitals. The *foramen magnum* is large and nearly circular. The posttemporal fossae are small slits, bounded dorsally by the supraoccipital and ventrally by the paroccipital. The lateral outer border of the skull is formed by the squamosal and medial to this edge lies a shallow 'auditory' groove that has its inner wall formed by a strong curved ridge formed wholly by the squamosal with no participation by the paroccipital and tabular as in *Struthiocephalus*. Ventrally the condyles of the quadrates lie far anteriorly of the plane of the occiput. In occipital view the basioccipital part of the condyle forms the median part of the ventral edge, which is laterally continued by the quadrate ramus of the pterygoid, the

quadrate condyles and the quadratojugal. Looking at the occiput at right angles to the plane in which the alveolar borders of the maxillaries lie, much of the surfaces of the parietal, postorbitals, postfrontals and frontal is seen.

The basioccipital (B.O.) in occipital view shows a T-shaped surface with the stem, lying in the median line, excavated by a shallow groove leading into the *foramen magnum*, and the cross-member forming the ventral edge of the condyle carrying a large notochordal pit. The dorso-lateral corners of the condylar surface are formed by the exoccipitals.

Each exoccipital (E.O.) forms a small triangular part of the occipital face lying lateral to the lower half of the *foramen magnum* and then stretches posteriorly to overlap on to the dorso-lateral corner of the condyle.

The supraoccipital (S.O.) is a low, broad bone forming the upper half of the border of the *foramen magnum*. Laterally it tapers to a point extending just past the posttemporal fossa, and forms its dorsal edge. Ventrally its edge is overlapped by the exoccipital, dorsally it meets the interparietal and, laterally, the tabular with only small contacts with the paroccipital on both sides of the posttemporal fossa. The median occipital ridge is low or absent on the supraoccipital but is a prominent feature on the interparietal.

The interparietal (dermosupraoccipital) (I.P.) is the main median bone of the occiput. It is a fairly large bone—nearly square in outline—and carries a strong and prominent ridge along the median line of the occiput. Lateral to this ridge its surface is shallowly to very deeply excavated. Dorsally it forms the strong rounded edge of the middle part of the upper occipital edge, meeting the parietal on the dorsal surface of the skull.

The tabular (T.) is the bone with the largest surface of all the bones of the occiput. Dorsally it forms the major part of the strong rounded overhanging edge of the occiput and meets the parietal on the dorsal surface of the skull and on the dorsal face of the posttemporal arch. Dorso-laterally it meets the upsweeping process of the squamosal along the posterior edge of the posttemporal arch. It stretches far laterally but does not contribute to the formation of the ridge lying medially of the 'auditory' groove. Ventrally it overlaps the dorsal paroccipital edge lateral to the posttemporal fossa.

The paroccipital (P.Oc.) in occipital view is seen to be a strong bar medially abutting against the basioccipital and overlapped by the exoccipital and stretching far laterally to meet the squamosal mesial of the 'auditory ridge' and overlapping the dorsal part of the posterior face of the quadrate, which it buttresses very firmly. Its proximo-ventral corner is seen to form the posterior part of the rim of the *fenestra ovalis*. In occipital view it obscures much of the stapes—especially that bone's distal end.

The quadrate (Q.) in occipital view presents a roughly rectangular face with, ventrally, a pair of strong rounded knobs separated by a groove forming the articulatory condyles for the articular. Laterally the quadrate is overlapped by the squamosal and flanked by the quadratojugal. Dorsally the posterior face of the quadrate is overlapped by the distal end of the par-

occipital firmly applied to it. Medially the short anterior process of the quadrate is firmly overlapped by the distal end of the quadrate ramus of the pterygoid and dorsally to this the postero-distal process of the stapes is securely applied to the posterior face of the quadrate. Latero-ventrally to the postero-distal corner of the stapes the quadrate carries a low rounded tubercle. An oval quadratic foramen cuts a notch into the lateral edge of the quadrate.

The quadratojugal (Q.J.) in posterior view presents a small triangular face; its inner edge is notched by the oval quadratic foramen; dorsally the squamosal overlaps the posterior face of the quadratojugal.

The stapes (St.) can only be partly seen in occipital view, as the paroccipital obscures its upper and dorso-distal corner. The stapedial foramen can just be seen. The postero-distal process, directed towards the tubercle of the quadrate, is seen to be applied to the quadrate and firmly wedged in between the paroccipital and the quadrate and its distal end securely overlapped by the end of the quadratic ramus of the pterygoid. Proximally the footplate of the stapes fits into the ventrally situated *fenestra ovalis*, which has the posterior part of its rim formed by a downgrown process of the paroccipital and its ventral edge formed by the basioccipital.

The stapes is seen to lie diagonally, with its proximal end appreciably higher than its distal end.

Finally, the quadrate ramus of the pterygoid (Pt.) is seen to be firmly applied to the postero-medial face of the anterior process of the quadrate and overlapping the ventro-distal end of the stapes.

The Ventral Surface of the Skull

The ventral surface of the skull in the Tapinocephalidae is well exposed in only one specimen of *Tapinocephalus* (S.A.M. 2344), fairly well in one specimen (B.M. R.3594) of *Mormosaurus*, poorly in another specimen (S.A.M. 9082), whereas little is known of this aspect in *Phocosaurus* and *Keratocephalus*.

The bones of the palate and the *basis cranii* lie in practically the same plane, with the fairly weak lateral pterygoidal rami extending ventral to this plane, and the bones of the suspensorium lying still further ventrally. Striking is the very anterior position of the articulatory condyles of the quadrates, which lie far anterior to the plane in which the basioccipital condyle lies, nearly half-way up the ventral surface of the skull. The subtemporal fossae are small, short but fairly wide, the *choanae* are large, short but wide and the inter-pterygoidal vacuity is a fairly narrow slit just extending anteriorly to between the posterior end of the prevomers. A very small suborbital opening lies between the palatine and transversum. In the projection on to the plane of the maxillary alveolar borders the surface of the occiput is seen as the occiput makes an angle of more than 90° with this plane.

The basioccipital (B.O.) is, in ventral view, seen to form the greater part of the occipital condyle. The condyle is a strong rounded knob with its postero-ventral corners formed by the exoccipitals. The basioccipital has a fairly large

and deep notochordal pit facing postero-ventrally so that from the atlas the skull would hang downwards. Anteriorly to its condylar part the basioccipital has a short but apparently wide face, which is slightly tilted down in anterior direction and there carries two low tubera lying just posterior to the basioccipital-basisphenoidal suture. The lateral edge of these tubera forms the ventral rim of the *fenestra ovalis*, which thus lies far ventrally. Between the lateral corner of the tuber and the jugular foramen the basioccipital abuts against the antero-medial corner of the paroccipital. Further posteriorly the basioccipital meets the flange of the exoccipital, which overlaps the proximal part of the paroccipital face.

The basisphenoid (B.S.) posteriorly meets the basioccipital in a digitate transverse suture at an angle so that the ventral surfaces of these two bones subtend a very obtuse angle. On its postero-lateral processes the basisphenoid carries low tubera and their postero-lateral edge forms the antero-ventral rim of the *fenestra ovalis*. The anterior extension of the basisphenoid, wedged in between the quadratic rami of the pterygoids, is short. Along the median line the basisphenoid carries a low keel lateral to which, near the anterior edge of the bone, lie the internal carotid foramina. Lateral to each tuber lies the foramen for the carotid.

The paroccipital (P.Oc.) is a strong and massive bone which forms a strong and firm connecting link between the cranial base (more particularly the basioccipital, with the exoccipital overlapping on to its ventral and ventro-posterior face) and the tabular, lying dorsally, and the squamosal, laterally, and its firm support of the quadrate is most important. Its antero-lateral corner also affords a firm support to the postero-distal end of the stapes, and its antero-medial corner forms the postero-ventral part of the rim of the *fenestra ovalis*.

Concomitant with the forward shift of the quadrate a rotation of the paroccipital on its long axis has taken place with the result that the paroccipital presents a much greater face in ventral view than it presents in occipital view.

The two pterygoids (Pt.) together form a relatively small part of the centre of the ventral surface of the skull. As each pterygoid has no anterior process, only a weak lateral flange, a short quadrate ramus and in the median line extending only a short distance posteriorly, it is a not very prominent bone. Posterior to the interpterygoid slit the pterygoid meets its fellow in the median line to form a low keel, which is continuous with that formed by the basisphenoids. Lateral to this median keel each pterygoid is deeply excavated to form a wide and deep diagonally situated groove, which is then laterally bounded by the quadrate ramus, which is a deep sheet of bone lying obliquely in the skull and this sheet lies nearly at right angles to the plane of the palate. Although the quadrate ramus of the pterygoid is comparatively short, it has a large and firm overlap on the quadrate, being firmly applied to the mesial face of the anterior quadratic process and extending well posterior of the plane in which the condyle of the quadrate lies. The upper edge of the quadrate

ramus lies ventrally to, but with a fairly firm contact with the anterior part of the distal end of the stapes, which, passing above it, is firmly applied to the mesial face of the anterior quadratic process.

The quadratic ramus is connected to the lateral ramus by a strong web of bone.

The lateral ramus of the pterygoid is weak and does not descend far ventrally nor extend much laterally, which is in strong contrast to the condition in the carnivorous Titanosuchia and Anteosauria. It is also relatively weaker than in the Moschopids, but about the same as in the Struthiocephalids. Laterally the flange is supported by the robust transversum which, because of the small lateral extent of the lateral ramus, presents a large ventral face. This is also seen in *Struthiocephalus*. Anteriorly the pterygoids do not appear to extend anterior to the plane in which the anterior edge of the lateral rami lie.

The transversum (Tr.) is a robust bone forming a strong link between the lateral ramus of the pterygoid and the side wall of the skull, being firmly buttressed against the inner face of the jugal and, to a lesser degree, against the maxilla. Anteriorly it meets the palatine in a straight suture, with only a small suborbital foramen separating them.

The palatine (Pal.) stretches antero-laterally from the anterior edge of the transverse pterygoid ramus as a thick sheet of bone to form much of the lateral border of the *choana*, and has its lateral edge applied to the inner maxillary surface, where it flanks the alveolar border. In the median line a tongue of the prevomers apparently prevents the two palatines from meeting each other. On its postero-median corner the palatine carries a mound-like ridge which does not, however, appear to be dentigerous.

The prevomers (vomers) (P.V.) are strong but relatively short bones, which together form a massive interchoanal bar. Their anterior bevelled ends underlie the inner face of the premaxillaries. Posteriorly they widen to meet the palatines postero-laterally, but in the median line apparently send a tongue posteriorly which is intercalated between the medial edges of the palatines. Anteriorly, along the median line, the interchoanal bone is grooved, whereas posteriorly a low keel is developed.

The premaxillary (P.M.) has a very massive alveolar face but in all the known specimens little of the teeth is known and where infilled alveolar sockets can be seen they appear to be irregular with some indication of replacement lingually.

The maxilla (M.) has its alveolar border anteriorly massive and wide but it then tapers rapidly in posterior direction with a sharp edge continuous with the sharp ventral edge of the jugal. Little is known of the teeth but it would appear that they were even more degenerate than those on the premaxilla.

The jugal (J.) in ventral view presents a sharp ventral edge curving sharply downwards to meet the quadratojugal, and an internal face forming, together with the transversum, the outer border of the subtemporal fossa. Anteriorly it meets the massive transversum in a sigmoid suture.

The quadrate (Q.) in ventral view presents its articulatory surface as a very prominent feature. The condyle is bipartite with two fairly robust rounded cotyli separated by a shallow groove. The edges of the cotyli overhang both the anterior and posterior faces of the dorsal part of the quadrate. Running obliquely inwards from the inner cotylus is the anterior quadratic process and it is against its mesial face that the quadrate ramus of the pterygoid is very firmly applied. Lateral to the outer cotylus the quadrate edge has a rounded step up before meeting the quadratojugal, which is applied to its outer surface, with a fairly small *foramen quadrati* lying half-way along the suture.

Since the quadrate lies in a forwardly inclined plane much of its posterior face is seen in ventral view. On this surface there is a small low tubercle above the inner cotylus, to which the postero-lateral sharp process of the stapes is all but applied. In ventral view it is very clearly shown how firmly the more dorsal part of the quadrate is overlapped by the down-sweeping squamosal outwardly and inwardly by the strongly down-sweeping antero-ventral part of the strong paroccipital. Above the upper edge of the quadratic ramus of the pterygoid the distal end of the stapes abuts very firmly against the mesial face of the quadrate. Another part of the distal end of the stapes passes above the antero-lateral corner of the paroccipital to abut against the quadrate.

The quadratojugal (Q.J.) in ventral view is seen to be a small element wedged in between the outer face of the quadrate and the lower overlapping edge of the down-sweeping squamosal. A small *foramen quadrati* notches the mesial edge of the quadratojugal.

The squamosal (Sq.) is seen to form the angle of the 'cheek' and sweeping downwards it overlaps the quadrate and quadratojugal. The strong and prominent 'auditory' ridge is well shown with the 'auditory' groove lying lateral to the ridge.

The stapes (St.) lies obliquely; from the ventrally situated *fenestra ovalis* it is inclined both forwards and downwards. In the ventral view the stapes is seen to present two distinct faces. The ventral face is elongate with a central waist, a knoblike proximal end firmly fixed in the *fenestra ovalis* and an expanded distal end, which has a long pointed postero-lateral process terminating just above the tubercle on the posterior face of the quadrate and wedged in between the quadrate ramus of the pterygoid and the paroccipital. The posterior face, which is perforated by the round stapedial foramen, is triangular in outline, with its base applied to the quadrate, after passing outwards above the downwardly grown antero-ventral corner of the paroccipital.

By this rather complex system of wedging it is clear that the distal end of the stapes is all but wholly immovable.

The tabulars (T.), interparietal (I.P.) and the supraoccipital (S.O.) are visible in ventral view, because the occiput-face is inclined somewhat anteriorly from above downwards. These bones lie well posterior to the basioccipital condyle with the first two forming the posterior edge of the skull, which is slightly concave in *Tapinocephalus* and *Mormosaurus*, convex in *Phocosaurus* and

Keratocephalus (except in one specimen), whereas in the Struthiocephalids this edge is nearly straight or convex, in Moschopids convex and deeply concave in the Titanosuchia and very deeply concave in the Anteosauria.

The Braincase in Lateral View

Hitherto the braincase of a specimen of *Tapinocephalus atherstonei* has been figured[1] and now a specimen of *Keratocephalus*, in which both sides of the braincase have been exposed, is to be described.

The braincase in *Keratocephalus* is short and low with the nearly horizontal *basis cranii* formed by the basioccipital and basisphenoid.

The posterior part of the side wall is formed by inwardly directed plates of the squamosal, supraoccipital and paroccipital. The antero-ventral corner of the paroccipital meets the basioccipital to form the posterior part of the rim of the *fenestra ovalis*. The anterior half of the rim of the *fenestra ovalis* is formed by the basisphenoid.

Anterior to the plates of the squamosal, supraoccipital and paroccipital lie the prootic and epipterygoid, but the sutures here cannot be determined with certainty, but appear to lie where indicated in broken line in the figure (fig. 15).

The epipterygoid (Ep.) appears to be incorporated into the side wall with the obliteration of the *cavum epiptericum*. Its base rests on the pterygoid with possibly a small contact with the basisphenoid.

The posterior edge of the epipterygoid has not been determined with any degree of certainty, but probably lies where indicated by broken line in the figure, in which case it is firmly applied to the antero-internally directed plates of the paroccipital and supraoccipital.

Dorsally the dumbbell-shaped vacuity for the trigeminal nerve (V.) causes the epipterygoid to bifurcate; the posterior *processus oticus* meets the prootic, whereas the anterior *processus ascendens* meets the under surface of the parietal with its upper edge and the sphenethmoid with the upper part of its anterior edge. The lower half of the anterior edge of the epipterygoid forms the posterior edge of the fenestra leading into the *fossa hypophyseos*.

The prootic (Pot.), as I have tentatively determined its limits, is a small bone wedged into the dorso-posterior corner of the side wall of the braincase. Dorsally it meets the parietal just mesial to this bone's contact with the postorbital. Posteriorly its edge is applied to the plate of the squamosal. Its ventral edge meets the supraoccipital and the upper edge of the *processus oticus* of the epipterygoid. Its anterior edge is applied to the posterior edge of the *processus ascendens* of the epipterygoid. The prootic forms the upper edge of the trigeminal foramen.

Of the parasphenoid (Ps.) only the dorsal branch is present, the anterior horizontal branch is not preserved. It stands with its thickened base on the upper surface of the basisphenoid and also, anteriorly, on the pterygoids. Immediately above its base the bone narrows and then thickens in dorsal

direction so that its two lateral faces diverge to where the sphenethmoids rest on its outer dorsal edges. Its dorsal edge forms the anterior border of the fenestra of the *fossa hypophyseos*. In lateral view its dorsal edge meets the sphenethmoid in a long curved suture.

The sphenethmoid (Se.) forms a large part of the lateral wall of the braincase. In their postero-dorsal part the two sphenethmoids diverge to form a fairly narrow space to house the fore-end of the brain. Antero-dorsally the two thin sphenethmoidal plates are applied to each other to form a thin median septum, which apparently extends far anteriorly. Lateral to this median septum the sphenethmoid thus forms a recess, with the *tractus olfactorius* emerging in its posterior part. Dorsally of the recess in the sphenethmoid the under surface of the prefrontal is also deeply excavated and in this hollow the *bulbus olfactorius* was apparently housed.

Openings in the Side Wall of the Braincase

The fenestra (Hyp.) in the side wall for the *fossa hypophyseos* is fairly large, narrowly oval and is bounded by the parasphenoid, sphenethmoid, epipterygoid and ? pterygoid.

The fenestra for the trigeminus and abducens nerves (V.) is in outline dumbbell-shaped and it lies in the upper part of the epipterygoid and causes this bone to bifurcate into a *processus oticus* and *processus ascendens*.

The *truncus olfactorius* (I) emerges from the posterior corner of the recess in the sphenethmoid.

The foramen for the *n. trochlearis* (IV) pierces the sphenethmoid near its upper edge, just below its contact with the under surface of the frontal.

The foramen for the *n. opticus* (II) emerges from the upper part of a shallow depression lying in the sphenethmoid above the large *fenestra hypophyseos*.

A venous foramen (Ven.) pierces the prootic near its dorso-anterior corner just under this bone's contact with the parietal.

A foramen (Ca.) for the exit of the accessory branch of the carotid lies at the base of the parasphenoid.

The *fenestra ovalis* (F.O.) lies veiy low down and its rim is formed by the basioccipital, basisphenoid and paroccipital.

The Lower Jaw

In all the known Tapinocephalid genera the lower jaw is only adequately known in one specimen (S.A.M. 9082) of the genus *Mormosaurus*. Owing to deformation due to a simple shear the disposition of the elements of the lower jaw has been disturbed in that by telescoping the dentary has been forced backwards over the posterior bones.

Because of the great forward shift of the quadrate the lower jaw is very short, viz. at most only 60% of the maximum skull length. It is massive with a strong symphysis and the articulatory facets on the articular lie far ventrally—not much above the plane of the lower border of the jaw.

The dentary (D.) is the largest bone of the jaw with a strong, fairly square mentum and it forms by far the greater part of the strong symphysis. Its dorso-posterior end forms a very low coronoid process. On its alveolar border the dentition is very poorly preserved, with only three roots of teeth present anteriorly, but what appear to be emply sockets indicate that in life a fairly regular row of teeth must have been developed, with the anterior ones much larger than the posterior ones.

The splenial (S.) is a small bone with a weak symphysis with its fellow. At the symphysis there is a deep groove between dentary and splenial.

The angular (An.) presents a large external face. There is a deep angular notch and the reflected lamina (*lamina reflexa*) is a robust sheet of bone, which in its posterior part lies well away from the inner sheet of the angular to form a roomy *recessus angularis*. The reflected lamina forms the free postero-ventral edge of the jaw immediately anterior to the articular.

The surangular (S.A.) forms the curved dorso-posterior border of the jaw and this edge is rounded and robust. Dorsally the surangular abuts against the dentary and ventrally overlaps the articular. Internally the surangular presents a large face between the postero-ventral edge of the dentary, the articular and the postero-dorsal edge of the prearticular. This is the area of insertion of the *m. temporalis*.

The prearticular (Pa.) is a long sheet of bone anteriorly intercalated between the dentary and splenial, and posteriorly overlapping and strongly supporting the articular. The anterior half of its upper edge meets the coronoid and then posteriorly it has a free edge lingual to the insertion of the *m. temporalis*. Its ventral edge overlaps the inner face of the angular.

The articular (Ar.) is a robust bone wedged in and securely clasped externally by the surangular from above and the angular anteriorly, and internally by the prearticular. The articulatory facets on its dorso-posterior surface are situated low down. The outer transversely oval concave facet is separated by a low ridge from the inner nearly circular concave facet. A strong but short retroarticular process is directed postero-ventrally and to it was inserted a strong *m. depressor mandibulae*.

The coronoid (C.) is a flat sheet of bone applied to the inner face of the dentary and meeting the upper edge of the prearticular; it does not extend far posteriorly and the dorso-posterior corner of the lower jaw is formed by the dentary.

Taxonomic

Tapinocephalidae

Skull Characters of the Family

Skull large (length 488–585? mm.; breadth 400–540 mm.); relatively short and broad to fairly long and fairly narrow (length varies from 104–127?% of the breadth); relatively low to fairly low (height varies from 46–69% of the length); snout short to fairly short (snout length varies from 51–67% of the

total skull length); the snout is low to fairly high and fairly broad to broad (height of snout from 44–76% of the width of the snout).

The orbit lies in the posterior half of the skull.

The transition from the facial to the cranial surface sloping or very abrupt.

The dorsal cranial bones are strongly pachyostosed with the centres of thickening coalesced in all but one genus (*Keratocephalus*); this thickening occupies from 48–63% of the total median length of the skull. Postorbital bar wide to very wide and massive; the postfrontal does not form a prominent boss but its surface curves evenly on to the generally thickened dorsal surface; temporal fossa small with small to fairly small antero-posterior diameter; intertemporal region moderately to very wide (120–240 mm.); parietals enter upper border of temporal fossa; frontal excluded from the orbital border; lacrimal not reaching nasal.

Quadrate ramus of pterygoid is short.

Dentition in most cases feeble and undifferentiated.

Tapinocephalus

Skull Characters of the Genus

1. The preorbital length is 51–52% of the total median length; the snout is thus short (preorbital length 273 mm.) and it is broad (330 mm.) and low (144 mm.), with the height 44% of the width; the dorsal facial surface of the snout is short and does not extend to the plane of the anterior orbital border; the transition from the facial to the cranial surface is very abrupt.

2. The dorsal cranial bones are very strongly pachyostosed, with the centres of thickening coalesced and the transition on to the face is by an abrupt step along a U-shaped line; the thickening extends very far forward—well anterior to the plane of the anterior orbital border; along the median line the pachyostotic cranial roof is 339 mm. in length and this is 58–63% of the total median length of the skull; this great anterior extension is due to the greatly thickened naso-frontal boss, which does not, however, stand out dorsally above the general cranial surface. On the sharply up-bent face of the posterior end of each nasal there is a fairly deep hollow. The prefrontal is greatly thickened and this is confluent with the pachyostosis of the nasal and frontal and it overhangs the orbit forming the greatly thickened antero-dorsal part of the orbital border and limits direct anterior vision. The area around the pineal foramen is raised, but its general surface is lower than that of the surrounding bones.

3. The postorbital bar is very wide and very massive.

4. The posttemporal arch is very thick and the temporal fossa is small with its antero-posterior diameter greatly reduced.

5. The dorsal parietal surface is very broad (210-240 mm.) with in one specimen a narrow constricted bay to the temporal fossa; and the interorbital width is 88–100% of the intertemporal width.

6. Antero-posterior length of the parietal is fairly long (105–114 mm.); frontal fairly large.

7. The intersquamosal width is very great (495–540 mm.), and is 99–100% of the median length and the skull is thus nearly or quite as broad as long.

8. The quadrate is situated well forward; the mandibular length is 57% of the median length of the skull; the quadrate ramus of the pterygoid, although it extends to well posterior of the condyles of the quadrate and underlies the

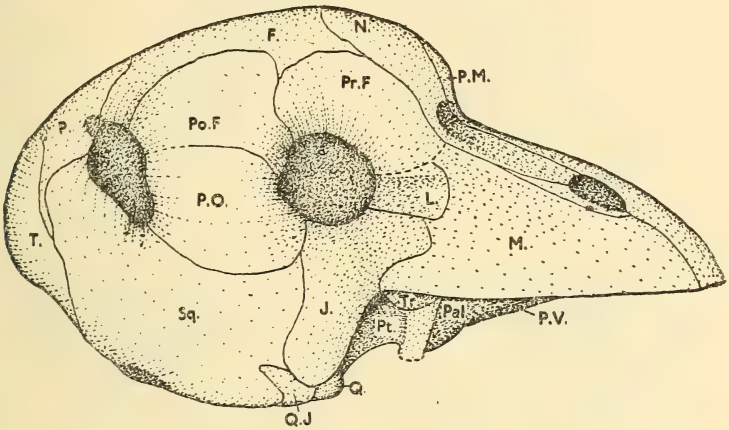

FIG. 1. *Tapinocephalus atherstonei.* Lateral view of skull. × $\frac{1}{6}$. S.A.M. 2344. Slight dorso-ventral compression not corrected.

Note.—All the figures in this paper are not perspective drawings but projections obtained by pantograph. Those labelled 'lateral view' are orthoprojections on to the median plane; 'dorsal' and 'ventral views' are orthoprojections on to the plane in which the alveolar borders of the maxillaries lie; the 'occipital views' are orthoprojections at right angles to the plane in which the maxillary alveolar borders lie.

distal end of the stapes, is short; the lateral pterygoid rami form a weak transverse bar of small width.

9. The dentition is poorly preserved but probably feeble.

Genotype. *Tapinocephalus atherstonei*, Owen 1876.

Specific diagnosis as for the genus.

Holotype. B.M. R.1705. Snout (there are also other parts of the skull associated). Near Janwillemsfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Atherstone.

Referred Specimens

A.M.N.H. 5626. Posterior half of a weathered skull. Ganskraal, Prince Albert. High *Tapinocephalus* zone. Coll. van Wyk.

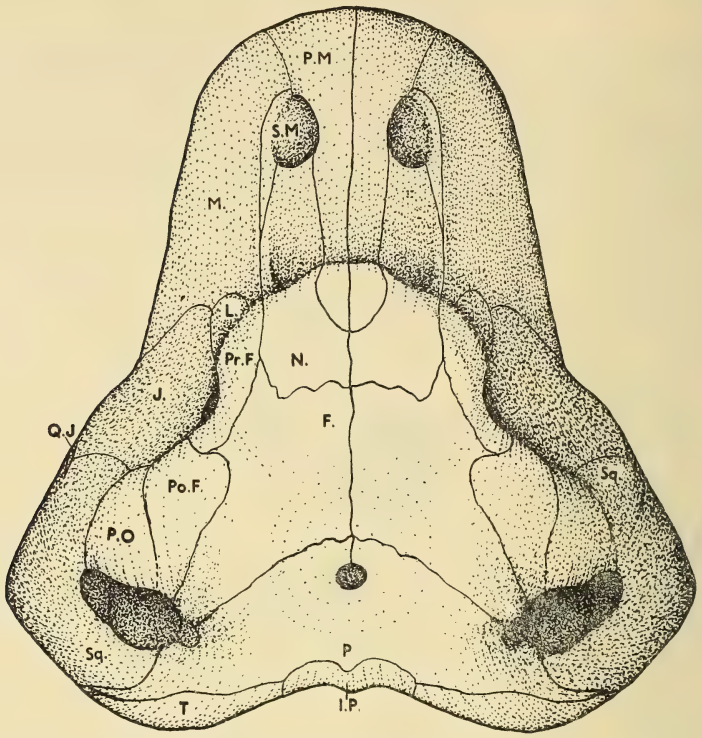

FIG. 2. *Tapinocephalus atherstonei.* Dorsal view of skull. × $\frac{1}{6}$. S.A.M. 2344.

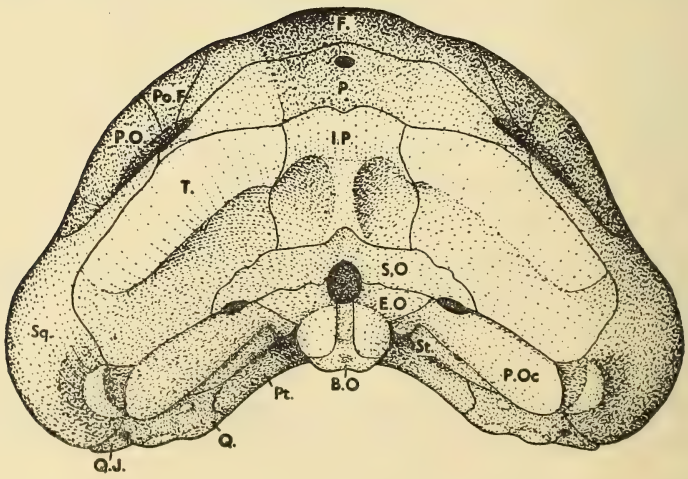

FIG. 3. *Tapinocephalus atherstonei.* Occipital view of skull. × $\frac{1}{6}$. S.A.M. 2344. Slight dorso-ventral compression not corrected.

S.A.M. 2344 (figs. 1–4). A good skull without lower jaw (with parts of the postcranial skeleton associated). Uitkyk, Beaufort West. Low *Tapinocephalus* zone. Coll. le Roux.

S.A.M. 11998 (fig. 5). Weathered piece of skull-roof. Sandriver, Beaufort West. Low? *Tapinocephalus* zone. Coll. Jack.

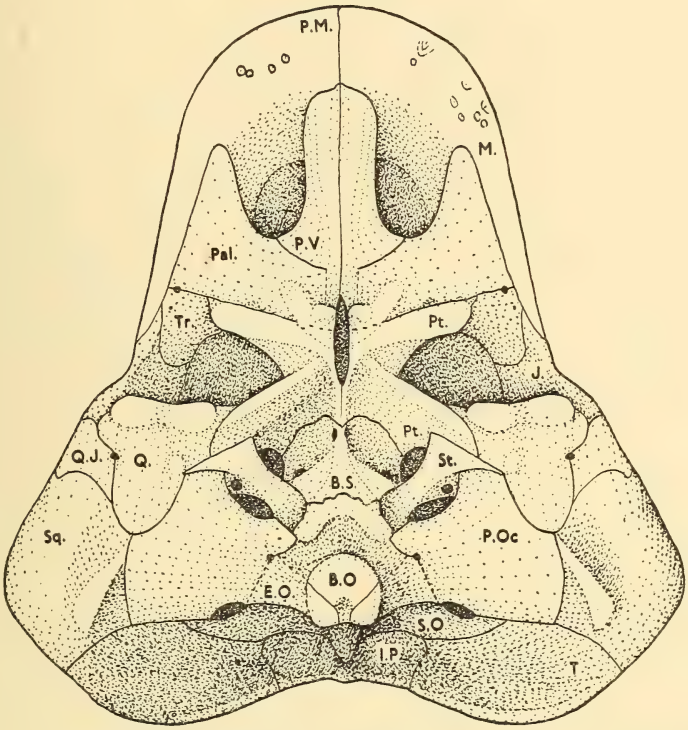

FIG. 4. *Tapinocephalus atherstonei*. Ventral view of skull. × $\frac{1}{6}$. S.A.M. 2344.

PHOCOSAURUS

Skull Characters of the Genus

1. The preorbital length is 54% of the total median length as reconstructed; the snout as reconstructed is thus fairly short (preorbital length 282? mm.) and it is fairly narrow (222 mm.) and fairly high (168 mm.) with the height 76% of the width; the facial surface of the snout is not very short and extends to the plane of the anterior orbital border; the transition from the facial to the cranial surface is not abrupt but slopes up evenly.

2. The dorsal cranial bones are strongly pachyostosed, with the centres of thickening coalesced and the transition on to the face is by a slope along an

indistinct indented line; the cranial thickening does not extend very far forward —just reaching the plane of the anterior orbital border; along the median line the pachyostotic cranial roof is 267 mm. in length and this is 51% of the total median length; this small anterior extension of the thickening is due to the fact that the naso-frontal swelling is situated posterior to the plane of the anterior

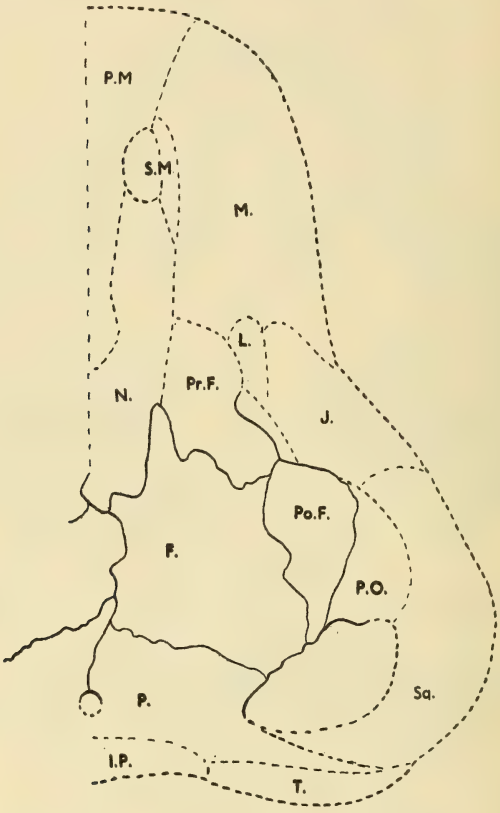

FIG. 5. *Tapinocephalus atherstonei.* Dorsal aspect of a weathered piece of the skull-roof. × $\frac{1}{6}$. S.A.M. 11998.

orbital border and to the fact that the anterior third of the prefrontal is unswollen; the naso-frontal boss is not very prominent, although it is higher than the general cranial surface. On the sloping face of the posterior part of the nasals there are a pair of shallow grooves. The posterior two-thirds of the prefrontal is strongly thickened and this is confluent with the pachyostosis of the nasal and frontal and overhangs the orbit, but the anterior orbital border is not greatly thickened. The surface around the pineal surface is depressed and lies lower than that of the surrounding bones.

3. The postorbital bar is fairly wide and massive.

4. The posttemporal arch is moderately thick and the temporal fossa is small and slitlike with its antero-posterior diameter very small.

5. The dorsal parietal surface is only moderately wide (177 mm.) and the interorbital width is 107% of the intertemporal width.

6. The antero-posterior length of the parietal is small (72 mm.); the frontal is not large.

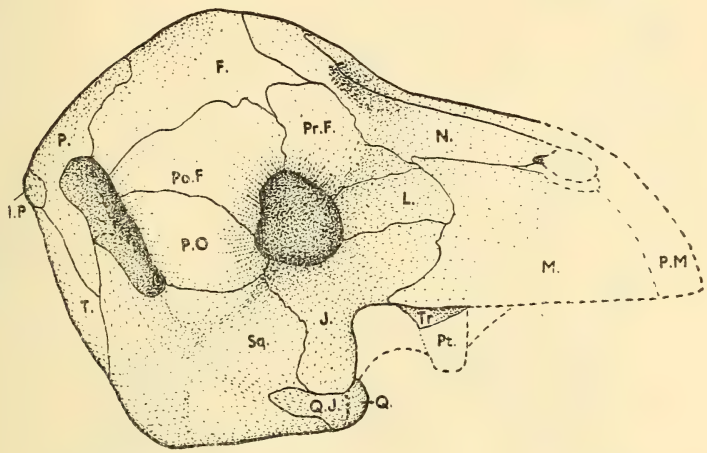

FIG. 6. *Phocosaurus megischion.* Lateral view of skull. × $\frac{1}{6}$. S.A.M. 11997.

7. The intersquamosal width is moderate (456 mm.); and the median length as reconstructed is 115% of the intersquamosal width and the skull is thus appreciably narrower than long.

8. The quadrate is situated very far forward; as reconstructed the mandibular length would be about 53% of the median length of the skull.

9. Dentition poorly known but probably feeble.

Genotype. *Phocosaurus megischion*, Seeley 1888.

Specific diagnosis as for the genus.

Holotype. B.M. 43525. Incomplete coraco-scapulae, humeri, ulna, incomplete pelvis and proximal half of the right femur. Varsfontein, Prince Albert. Middle *Tapinocephalus* zone. Coll. Atherstone.

Referred Specimens

S.A.M. 11997. Skull lacking tip of snout and without lower jaw (figs. 6, 7) with the distal end of a femur and radius and an incomplete ilium recently figured by me.[4] Locality and collector unknown.

S.A.M. 9103. A piece of the occiput and skull-roof. Droëfontein, Prince Albert. Low? *Tapinocephalus* zone. Coll. Boonstra.

MORMOSAURUS

Skull Characters of the Genus

1. The preorbital length is 57–58% of the total median length; the snout is thus fairly long (preorbital length 270–318 mm.) and fairly narrow to fairly broad (222–279 mm.) and fairly high (150–186 mm.), with the height 67–68%

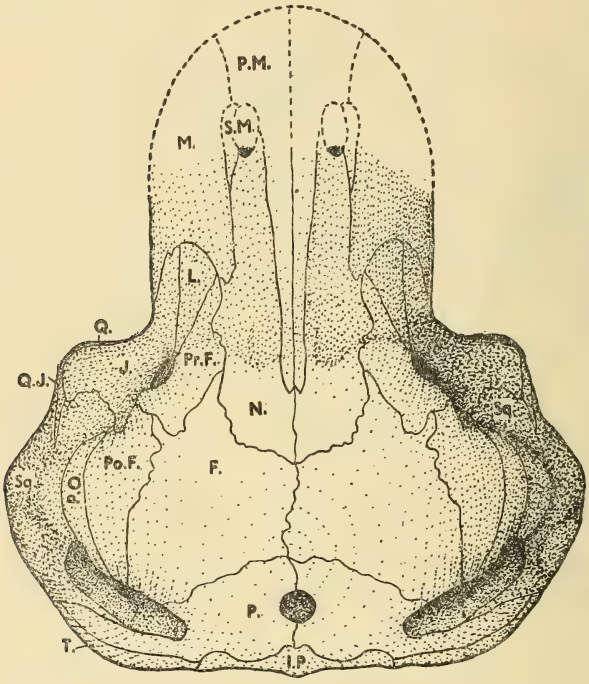

FIG. 7. *Phocosaurus megischion.* Dorsal view of skull. × $\frac{1}{6}$. S.A.M. 11997.

of the width; the facial surface of the snout is fairly short and it does not extend to the plane of the antorbital border; the transition from the facial to the cranial surface is abrupt.

2. The dorsal cranial bones are strongly pachyostosed, with the centres of thickening coalesced and the transition on to the face is by an abrupt step along a curved transverse line; the thickening extends far forward—anterior to the plane of the anterior orbital border; along the median line the pachyostotic cranial roof is 252–267 mm. in length and this is 48–55% of the total median length of the skull; this moderate anterior extension is due to the

thickened naso-frontal boss, which stands out well above the general cranial surface. On the upwardly sloping face of the posterior part of the nasals there are a pair of shallow depressions. The prefrontal is greatly thickened in its posterior three-quarters but not in its anterior one-quarter and it overhangs the orbit, but the antero-dorsal orbital border is not greatly thickened. The surface around the pineal foramen is lower than that of the surrounding bones.

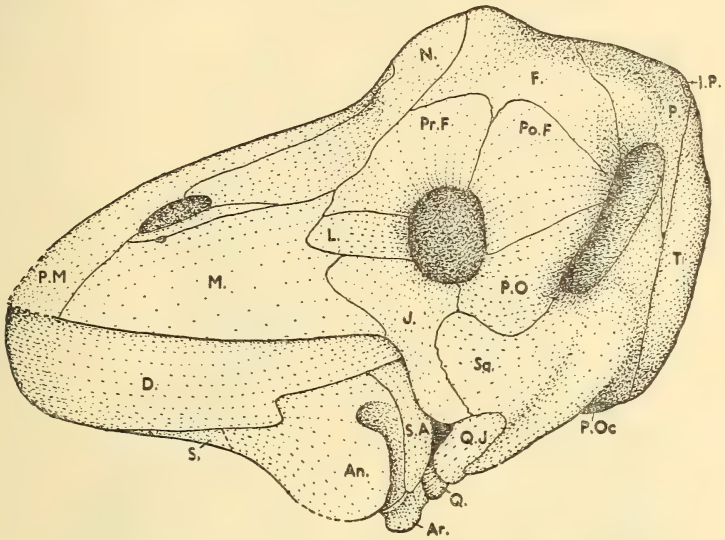

FIG. 8. *Mormosaurus seeleyi.* Lateral view of skull and lower jaw. × $\frac{1}{6}$. S.A.M. 9082. With correction of the simple shear the skull has suffered.

3. The postorbital bar is fairly wide and massive.

4. The posttemporal arch is thick and the temporal fossa is small with its antero-posterior diameter small to moderate.

5. The dorsal parietal surface is moderate to broad (150–200 mm.) and the interorbital width is 88–97% of the intertemporal width.

6. The antero-posterior length of the parietal is small (75 mm.) and the frontal is fairly large.

7. The intersquamosal width is moderate to great (438–477 mm.); and the median length is 105–115% of the intersquamosal width and the skull is thus slightly to appreciably narrower than long.

8. The quadrate is situated fairly far forward; the mandibular length is 59–64% of the median length of the skull; the lateral pterygoid rami weak but fairly wide.

9. The dentition is poorly preserved, but the anterior teeth in one specimen fairly robust.

Genotype. *Mormosaurus seeleyi*, Watson 1914.

Specific diagnosis as for the genus.

Holotype. B.M. R.3594. Skull without lower jaw. Koup. Low? *Tapinocephalus* zone. Coll. Seeley.

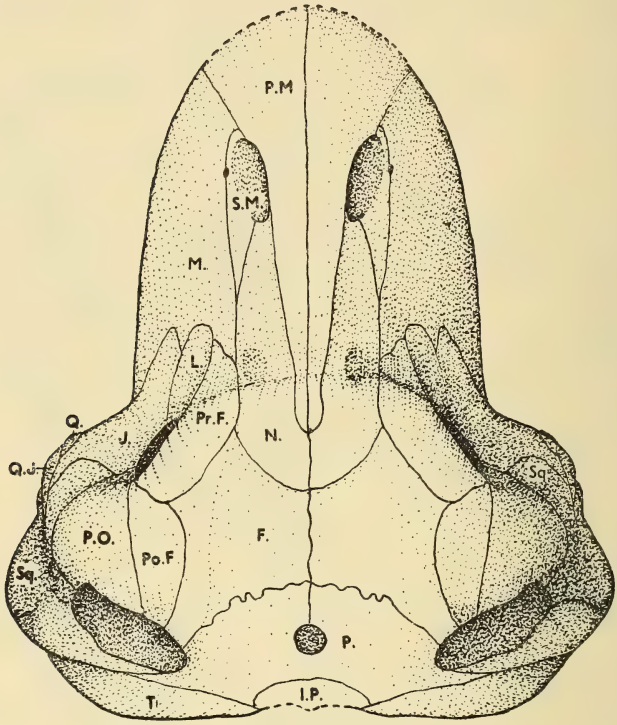

FIG. 9. *Mormosaurus seeleyi*. Dorsal view of skull. × $\frac{1}{6}$. S.A.M. 9082. With correction of the simple shear the skull has undergone.

Referred Specimen

S.A.M. 9082. A good but sheared skull with the left mandibular ramus (figs. 8–10). Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

KERATOCEPHALUS

Skull Characters of the Genus

1. The preorbital length is 51–67% of the total median length as reconstructed; no snout is fully known but the transition from the facial to the cranial surface is fairly abrupt.

2. The dorsal cranial bones strongly pachyostosed from centres which do not coalesce and the transition on to the face is not along a continuous line, being in parts abrupt, whereas in others gently sloping; along the median line the pachyostotic cranial roof is 260–330 mm. in length and this is 50–59% of the total median length as reconstructed; the great anterior extent of this thickening is concentrated in the high isolated naso-frontal boss, which stands out very prominently above the general cranial surface and also from the prefrontal swelling from which it is sharply demarcated by a shallow groove. The sloping face of the posterior part of the nasals does not appear to house any groove or

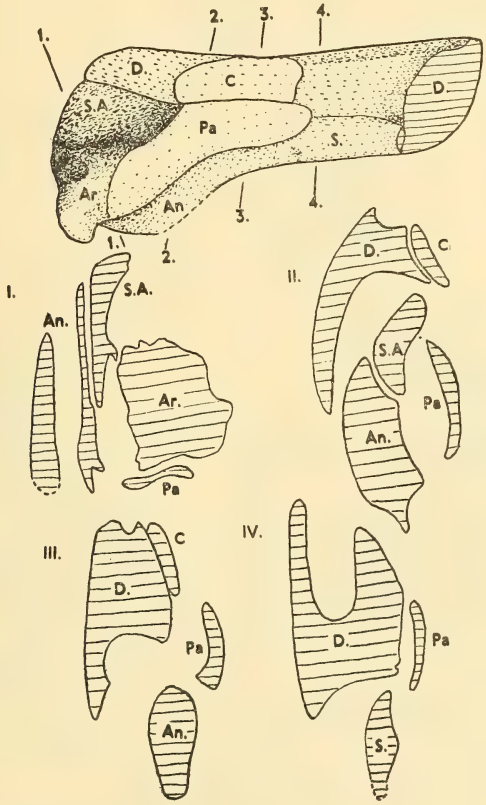

FIG. 10. *Mormosaurus seeleyi.* S.A.M. 9082.

Above. Lingual view of lower jaw. × $\frac{1}{6}$. With the telescoping of the bones corrected.

I–IV. Sections of the jaw, without correction of the telescoping the constituent bones have suffered from a simple shear. The levels of the sections are indicated by the figures 1–1, 2–2, 3–3, 4–4 in the top figure. × $\frac{1}{3}$.

deep hollow. The prefrontal, although thickened and overhanging the orbit, lies in a plane much lower than the naso-frontal boss, from which it is separated by a shallow, broad groove, and the antero-dorsal part of the orbital border is not greatly thickened.

The area around the pineal foramen forms a low to fairly high mound and this lies higher than the surface of the surrounding bones.

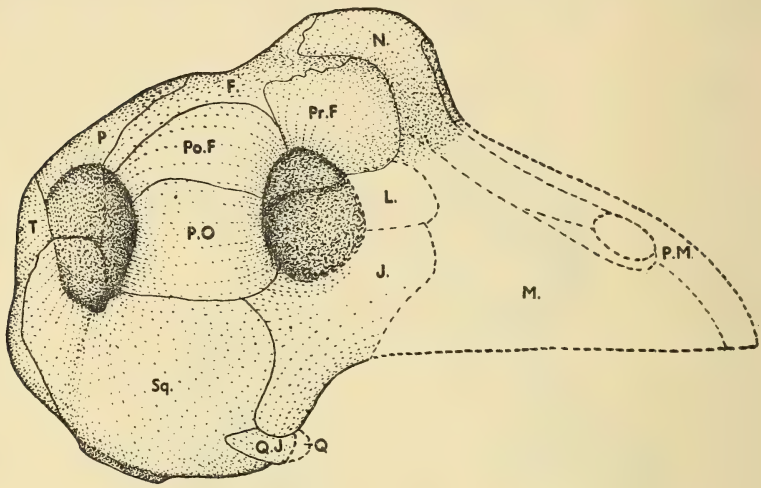

FIG. 11. *Keratocephalus moloch.* Lateral view of skull, with correction of the simple shear it has suffered. × ⅙. S.A.M. 11937.

3. The postorbital bar is wide to very wide and massive.

4. The posttemporal arch is moderately thick to thick and the temporal fossa is fairly large with a fairly large antero-posterior diameter.

5. The dorsal parietal surface is fairly narrow to moderately wide (120–171 mm.) and the interorbital width is 106–130% of the intertemporal width. In one specimen the lateral edge of the parietal surface is definitely pinched in as in some specimens of *Struthiocephalus*.

6. The antero-posterior length of the parietal is fairly long to long (102–135 mm.); the frontal is fairly short to fairly long.

7. The intersquamosal width is moderate to large (400?–480 mm.); the median length as reconstructed is 111–127% of the intersquamosal width and the skull is thus appreciably to much narrower than long.

8. The quadrate is situated fairly far forward.

9. In one specimen (S.A.M. 8946), where part of the jaw is preserved, the preserved sockets indicate a dentition as well developed as in some of the Struthiocephalids.

Genotype. *Keratocephalus moloch*, von Huene 1931.
Specific diagnosis as for the genus.
Holotype. Tübingen University No. ?. Parts of the skull and postcranial elements. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. von Huene.

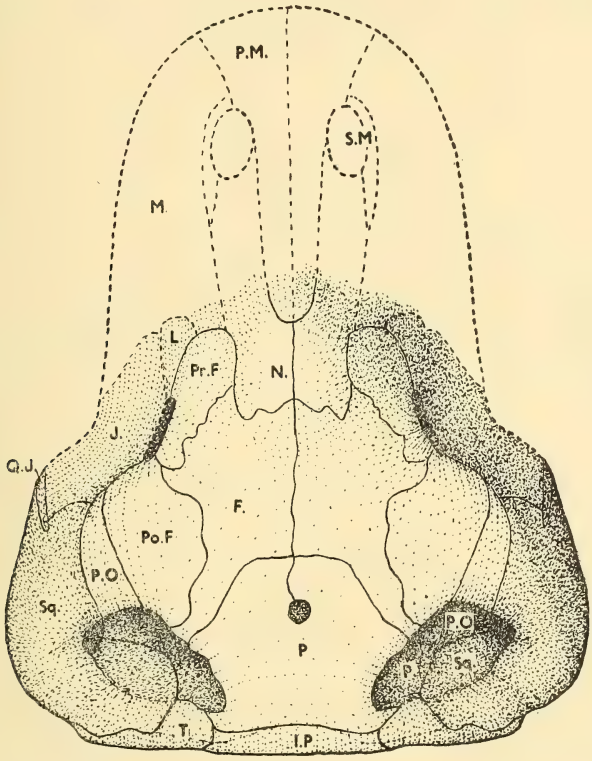

FIG. 12. *Keratocephalus moloch.* Dorsal view of the skull, with correction of the distortion caused by a simple shear. × $\frac{1}{6}$. S.A.M. 11937.

Referred Specimens

S.A.M. 10557. Good skull-roof. Fraserburg Boad, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra. This specimen was figured by me in 1951.[2]

S.A.M. 11937. The posterior two-thirds of a skull (figs. 11, 12) with parts of the postcranial skeleton recently figured by me.[4] Buffelsvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Marais.

S.A.M. 11294. The weathered and incomplete posterior part of a skull with the sides of the braincase exposed (figs. 13–15). Boesmansrivier, Beaufort West. Middle *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 8946. The incomplete posterior half of the skull (figs. 16, 17) with some limb bones. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

TAUROPS

As only the snout of this genus is known it can only, because of its size, be tentatively placed in the Tapinocephalidae.

The teeth, 14 in number, are typically Tapinocephalian with the largest three implanted in the premaxilla and the others regularly decreasing in size

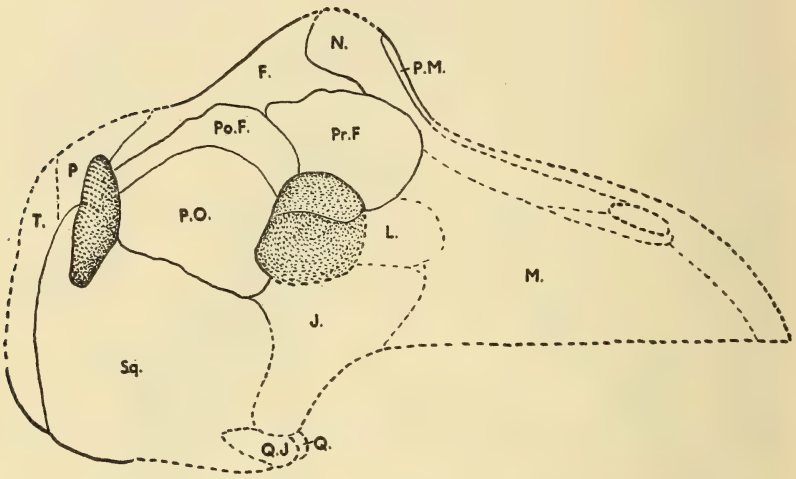

FIG. 13. *Keratocephalus moloch.* Lateral view of skull. × ⅛. S.A.M. 11294.

in posterior direction. This apparently regular set is accompanied by a set of replacing teeth. The lower jaw teeth are very similar to the upper set.

If this specimen has been correctly referred to the Tapinocephalidae then there is further indication that in some genera, at least, the teeth are not degenerate as they appear to be in those genera where good skulls are known.

Genotype. *Taurops macrodon*, Broom 1912.

Specific diagnosis as for the genus.

Holotype. A.M.N.H. 5610. A snout with teeth. Boesmanshoek, Laingsburg. Low? *Tapinocephalus* zone. Coll. Whaits.

PELOSUCHUS

On the basis of some features exhibited by the bones of the postcranial skeleton preserved I have recently[4] included *Pelosuchus* in the Tapinocephalidae.

Of the skull only a weathered dentary is preserved and this shows that in the dentary, at least, the dentition is typically Tapinocephalian, with large

anterior teeth, and that in posterior direction the teeth evenly decrease in size.

If this dentary is thus correctly referred to the Tapinocephalidae then in one genus of the family at least a full set of regularly placed teeth is present.

Genotype. *Pelosuchus priscus*, Broom 1905.

Specific diagnosis as for the genus.

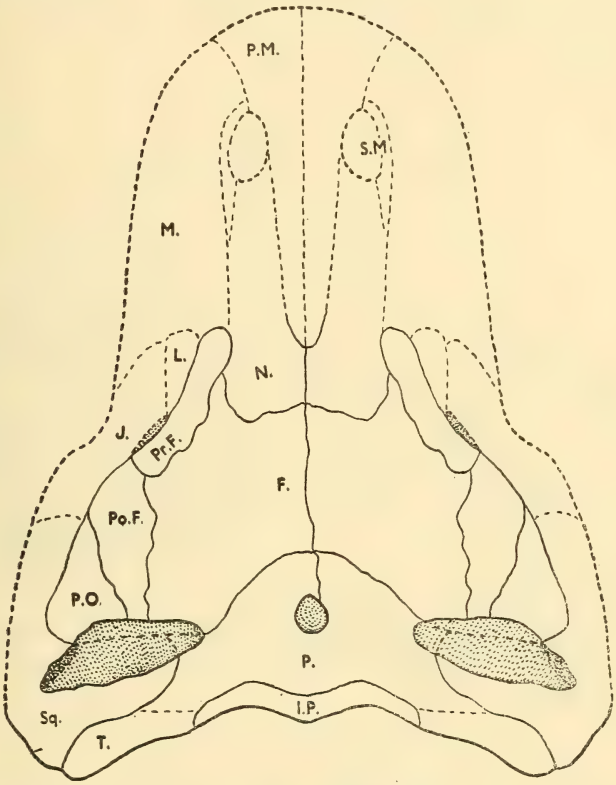

FIG. 14. *Keratocephalus moloch.* Dorsal view of skull. × $\frac{1}{6}$. S.A.M. 11294.

Holotype. S.A.M. 918. A dentary, with part of a scapula, coracoid, a fairly good femur and a distorted tibia. Bokfontein, Prince Albert. Middle? *Tapinocephalus* zone. Coll. du Plessis.

DISCUSSION

As I am nearing the completion of my study of the cranial structure in the other groups of the South African Tapinocephalia and hope to have a comparative account ready in the near future, only some points in the structure of the skull of the Tapinocephalidae call for discussion at this stage.

Age in the Skull of the Tapinocephalidae

In the Moschopid, *Moschops* and the Struthiocephalid, *Struthiocephalus*, where a fair number of skulls is available for comparative study, there is evidence (somewhat obscured by the possibility of sexual dimorphism) that with increasing age the pachyostosis is intensified. But there is also evidence that the increased pachyostosis during the lifetime of the individual is paralleled by a very similar increased pachyostosis during the evolution of the group.

In the Tapinocephalids we still have insufficient material to supply the necessary evidence on these matters.

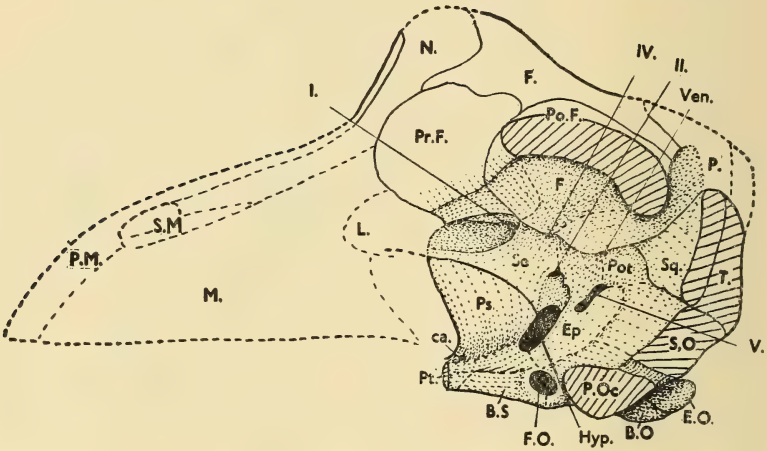

Fig. 15. *Keratocephalus moloch.* Lateral view of braincase, incorporating features of both right and left sides. × $\frac{1}{6}$. S.A.M. 11294.

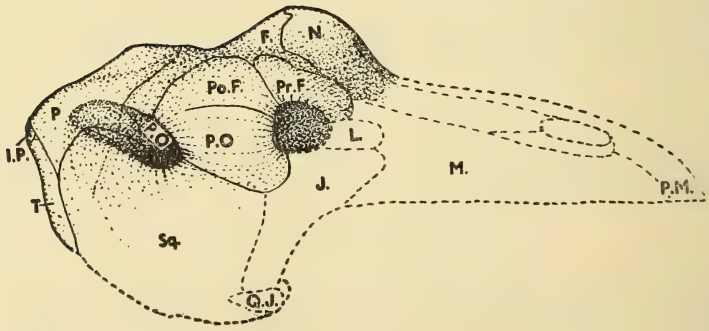

Fig. 16. *Keratocephalus moloch.* Lateral view of skull. × $\frac{1}{8}$. S.A.M. 8946. Dorso-ventral compression uncorrected.

It is quite clear that the skull S.A.M. 2344 is that of an old reptile. The sutures are all very much closed, and the poor preservation of the dentition is due to gerontism and not to the postmortem loss of teeth prior to petrifaction, in which case the alveoli would be matrix-filled and clearly determinable, whereas in fact separate alveoli are rarely visible. Now, the pachyostosis in this skull is very great and can also be considered to be due to its old age, but in A.M.N.H. 5626 and S.A.M. 11998, with very open sutures, the pachyo-

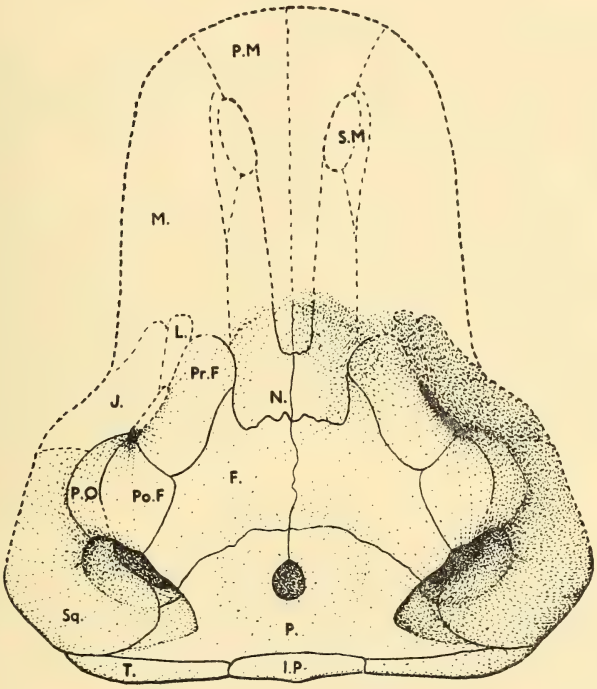

FIG. 17. *Keratocephalus moloch.* Dorsal view of skull. × $\frac{1}{6}$. S.A.M. 8946.

stosis is also very great so that it would appear that the great pachyostosis is not a function of age but a phyletic character.

In the one well-known skull of *Phocosaurus*, although the sutures are fairly open, the pachyostosis is fairly great and this again points to the phyletic character of the pachyostosis.

In the two known skulls of *Mormosaurus* the sutures are not open, the teeth are not strongly developed (especially posteriorly) and the pachyostosis is great, which apparently points to the pachyostosis being a character of old age.

In the five known skulls of *Keratocephalus* the dentition is apparently well developed, with no indication of degeneracy or gerontism; the sutures are

mostly fairly open and the centres of pachyostosis tend to remain uncoalesced. But, although these skulls may thus be thought to be of fairly young animals, there is a considerable difference in size (length as reconstructed varying from 488–585 mm. and breadth from 400–480 mm.) which, apart from possibly indicating males and females, would point to stages of growth or age within the species.

My conclusion is that the genera *Keratocephalus*, *Mormosaurus*, *Phocosaurus* and *Tapinocephalus* cannot be considered to represent growth stages of a single genus, but represent distinct directions of phyletic development.

Some Palaeobiological Conclusions

In my recent account[4] of the Deinocephalian girdles and limbs I pointed out that these skeletal parts indicate that the Tapinocephalidae were chiefly marsh dwellers, spending most of their time in the shallow ponds and pools and but seldom moving far on solid ground.

The nature of the dentition and the massiveness of the skulls described above lend further support to this view. With such a cumbersome body, a locomotor apparatus so ill adapted to efficient terrestrial ambulation and an extremely unwieldy masticating mechanism, with its rather feeble mandible hinged on to such a heavy and massive cranium, feeding on dry ground and chewing tough vegetable matter would have been extremely unlikely, whereas, with the heavy body and head buoyed up in the water, feeding on soft and luscious marsh vegetation would be not only possible but imperative.

References

[1] Boonstra, L. D. 'Some Features of the Cranial Morphology of the Tapinocephalid Deinocephalians.' *Bull. Amer. Mus. Nat. Hist.*, 72, 2, 75–98. 1936.

[2] Boonstra, L. D. 'Kurze Notiz über den Schädel der Dinocephalen-Gattung *Keratocephalus* F. v. Huene.' *Neues Jb. Geol. Paläontol.*, Mh. 11, 341–344. 1951.

[3] Boonstra, L. D. 'The Cranial Morphology and Taxonomy of the Tapinocephalid genus *Struthiocephalus*.' *Ann. S. Afr. Mus.*, 42, 1, 32–53. 1953.

[4] Boonstra, L. D. 'The Girdles and Limbs of the South African Deinocephalia.' *Ann. S. Afr. Mus.*, 42, 3, 185–326. 1955.

[5] Broom, R. 'Notice of some new Fossil Reptiles from the Karroo Beds of South Africa.' *Rec. Albany Mus.*, 1, 5, 331–7. 1905.

[6] Broom, R. 'On the Skull of *Tapinocephalus*.' *Geol. Mag.*, 6, 543, 400–402. 1909.

[7] Broom, R. 'On some new Fossil Reptiles from the Permian and Triassic Beds of South Africa.' *Proc. Zool. Soc. Lond.*, 859–876. 1912.

[8] Broom, R. 'On *Tapinocephalus* and Two Other Dinocephalians.' *Ann. S. Afr. Mus.*, 22, 3, 427–438. 1928.

[9] Gregory, W. K. 'The Skeleton of *Moschops capensis* Broom, a Dinocephalian Reptile from the Permian of South Africa.' *Bull. Amer. Mus. Nat. Hist.*, 56, 3, 179–251. 1926.

[10] Haughton, S. H. 'On a Skull of *Tapinocephalus atherstonei*, Owen.' *Ann. S. Afr. Mus.*, 12, 1, 40–42. 1913.

[11] Huene, F. von. 'Beitrag zur Kenntnis der Fauna der südafrikanischen Karrooformation.' *Geol. Paläont. Abh., N.F.*, 18, 3, 159–228. 1931.

[12] Lydekker, R. 'Catalogue of the Fossil Reptilia and Amphibia in the British Museum (*Natural History*).' IV, 81–98. 1890.

[13] Owen, R. '*Descriptive and illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum.* Taylor and Francis, London. 1–86. 1876.

[14] Seeley, H. G. 'Researches on the Structure, Organization and Classification of the Fossil Reptilia. II. On *Pareiasaurus bombidens* (Owen), and the Significance of its Affinities to Amphibians, Reptiles and Mammals.' *Phil. Trans.* (B), 179, 59–109. 1888.

[15] Watson, D. M. S. 'The Deinocephalia, and Order of Mammal-like Reptiles.' *Proc. Zool. Soc. Lond.*, 749–786. 1914.

[16] Watson, D. M. S. '*Dicynodon* and its Allies.' *Proc. Zool. Soc. Lond.*, 118, 3, 823–877. 1948.

5. *Pareiasauriër-studies.* Deel XII. 'n Lewensrekonstruksie van *Bradysaurus seeleyi.* *Deur* LIEUWE DIRK BOONSTRA. (Met plaat IV.)

Tussen die jare 1927 en 1935 het ek die Pareiasauriërs van ons Karoo baie deeglik ondersoek en die resultate, veral die osteologiese en miologiese bevindinge, is hoofsaaklik in die reeks „Pareiasaurian Studies" in die Annale van die Suid-Afrikaanse Museum gedruk.

Nou laat ek hier 'n foto afdruk van 'n rekonstruksie van een van die soorte van die *Tapinocephalus*-sone, waarvan daar, veral uit die Koup, 'n hele aantal vry volledige geraamtes in die Museum bewaar word. Met hierdie lewenstoneel word die reeks „Pareiasauriër-studies" dan afgerond.

Die rekonstruksie van *Bradysaurus seeleyi* is lewensgroot gemaak en is 'n getroue weergawe van al die gegewens wat deur genoemde „Studies" byeengebring is.

Die plantegroei is nagemaak volgens die gegewens, ongelukkig maar karig, wat deur paleobotanikers beskikbaar gestel is.

Dat die tuiste van die Pareiasauriërs 'n laagliggende moerasagtige gebied was, weet ons van die anatomiese bou van hierdie diere, van die aard van die plantegroei en dit is, ten laaste, gegrond op die gegewens wat deur geoloë beskikbaar gestel is aangaande die aard en metode van die neersetting van die sedimente waaruit ons vandag die versteende geraamtes van die Pareiasauriërs kap.

Met die opstelling van hierdie paleobiologiese toneel is ek gehelp deur mnr. C. W. Thorne, wat verantwoordelik was vir die maak en opstel van die plante op die voorgrond, en deur dr. A. J. Hesse wat so geslaagd die agtergrond geskilder het.

AANGEHAALDE PUBLIKASIES

[1] Pareiasaurian Studies. „I. An Attempt at a Classification of the Pareiasuaria based on Skull Features." *Ann. S. Afr. Mus.*, 28, 1, 79–87. 1929.*

[2] Pareiasaurian Studies. „III. On the Pareiasaurian Manus." *Ann. S. Afr. Mus.*, 28, 1, 97–112. 1929.

[3] Pareiasaurian Studies. „IV. On the Pareiasaurina Pes." *Ann. S. Afr. Mus.*, 28, 1, 113–122. 1929.

[4] Pareiasaurian Studies. „V. On the Pareiasaurian Mandible." *Ann. S. Afr. Mus.*, 28, 1, 261–289. 1929.*

[5] „A Contribution to the Cranial Osteology of *Pareiasaurus serridens* (Owen)." *Ann. Univ. Stellenbosch*, 8, A, 5, 1–18. 1930.

[6] Pareiasaurian Studies. „VI. The Osteology and Myology of the Locomotor Apparatus. A.—Hind Limb." *Ann. S. Afr. Mus.*, 28, 3, 297–366. 1930.*

[7] Pareiasaurian Studies. „VII. On the Hind Limb of the Two Little-known Pareiasaurian Genera: *Anthodon* and *Pareiasaurus*." *Ann. S. Afr. Mus.*, 28, 4, 429-435. 1932.

* Met S. H. Haughton.

[8] Pareiasuarian Studies. „VIII. The Osteology and Myology of the Locomotor Apparatus. B.—Fore Limb." *Ann. S. Afr. Mus.*, 28, 4, 436–503. 1932.
[9] „The Phylogenesis of the Pareiasauridae: A Study in Evolution." *S. Afr. J. Sci.*, 29, 480–486. 1932.
[10] „Paleobiologiese Beskouinge oor 'n Uitgestorwe Reptielgroep (Pareiasauridae)." *S. Afr. J. Sci.*, 29, 487–494. 1932.
[11] „A Note on the Hyoid Apparatus of two Permian Reptiles (Pareisaurians)." *Anat. Anz.*, 75, 4/5. 1932.
[12] „The Geographical Distribution of the Pareiasaurs within the Karroo Basin." *S. Afr. J. Sci.*, 30, 433-435. 1933.
[13] „'n Metode in Gebruik vir die Opgrawing van die Pareiasauriers." *S. Afr. J. Sci.*, 30, 436–440. 1933.
[14] Pareiasaurian Studies. „IX. The Cranial Osteology." *Ann. S. Afr. Mus.*, 31, 1, 1–38. 1934.
[15] Pareiasaurian Studies. „X. The Dermal Armour." *Ann. S. Afr. Mus.*, 31, 1, 39-48. 1934.
[16] Pareiasaurian Studies. „XI. The Vertebral Column and Ribs." *Ann. S. Afr. Mus.*, 31, 1, 49–66. 1934.
[17] „On a Pareiasaurian Reptile from South Africa, *Bradysaurus whaitsi*." *Amer. Mus. Nov.*, 770, 1–4. 1935.

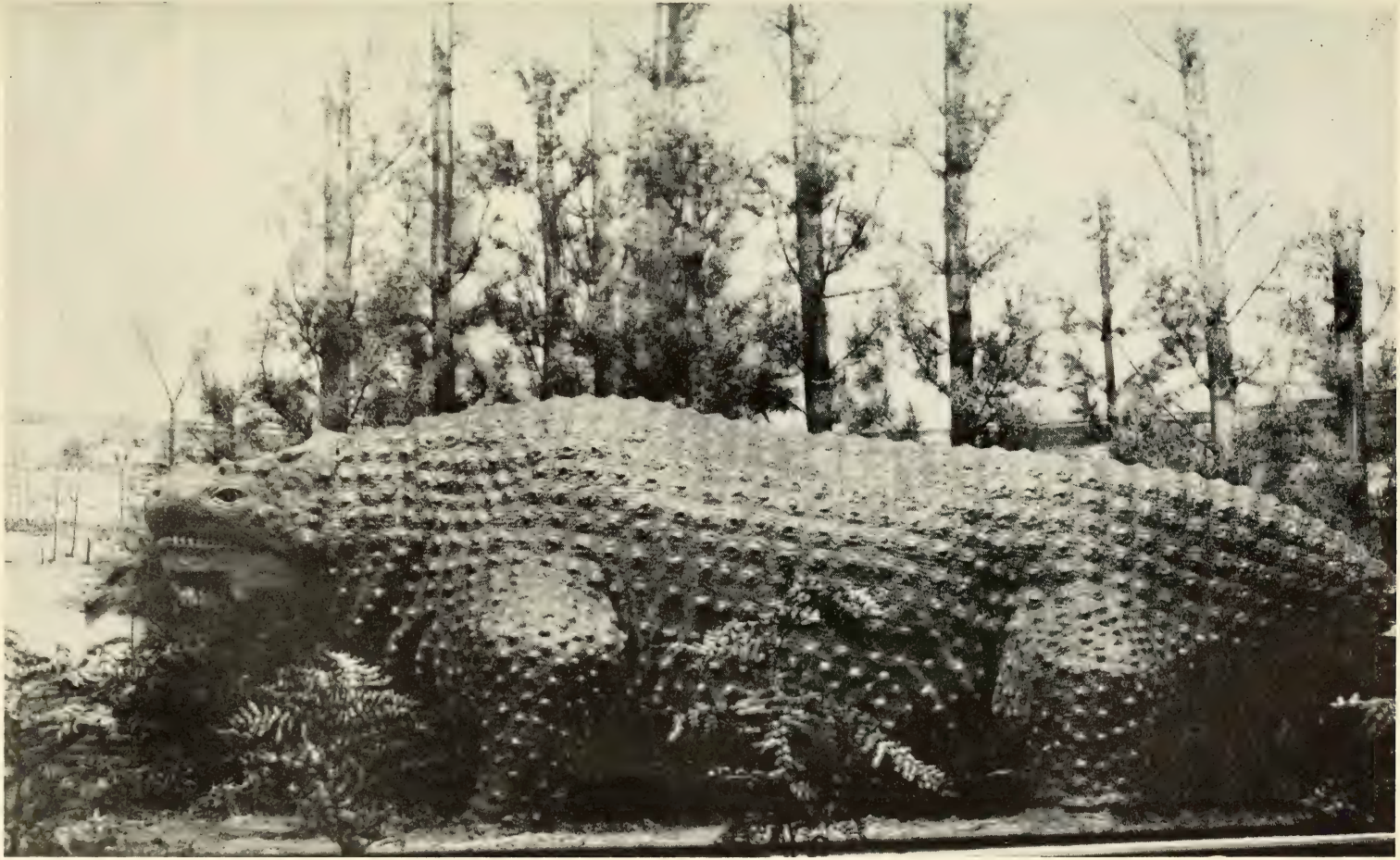

Foto: *Nas. Pers., Bpk.*

'n Lewensgrootte-rekonstruksie van *Bradysaurus seeleyi* in sy natuurlike omgewing soos opgestel in die Suid-Afrikaanse Museum.

The *ANNALS OF THE SOUTH AFRICAN MUSEUM* are issued in parts at irregular intervals as material becomes available.

Some volumes and parts are out of print, and others are only sold as parts of a set, or volume respectively. The prices of parts published prior to 1940 have been increased.

Out of print: Vols. I, II (Parts 1–3, 5, 7, 8), III (Part 1), V (Parts 1, 2, 5, 8, 9), VI (Part 1, Index), VII (Parts 1, 2, 3, 5), VIII, IX (Parts 1, 2), X (Part 2), XI (Parts 2, 7, Index), XXI (Part 1), XXIV (Part 2), XXXI (Parts 1–3).

Vol.			£	s.	d.
II.	1900–1902	Zoology and Geology (excl. Parts 1–3, 5, 7, 8)	1	2	10
III.	1903–1905	Zoology .. ..(excl. Part. 1)	1	16	0
IV.	1903–1908	Palaeontology	3	7	3
V.	1906–1910	Geology, Palaeontology, Zoology, Anthropology (excl. Parts 1, 2, 5, 8, 9)		16	3
VI.	1908–1910	Zoology .. .. (excl. Part 1, Index)	2	5	7
VII.	1908–1913	Palaeontology .. .. .. (Parts 4 and 6 only)		13	3
IX.	1911–1918	Botany .. .. .. (excl. Parts 1 and 11)	2	9	10
X.	1911–1914	Zoology .. .. (excl. Part 2)	4	13	5
XI.	1911–1918	Zoology .. .. .. (excl. Parts 2, 7, Index)	2	15	10
XII.	1913–1924	Palaeontology and Geology	4	17	3
XIII.	1913–1923	Archaeology and Zoology	3	10	10
XIV.	1915–1924	Zoology	3	6	7
XV.	1914–1916	Zoology	4	5	3
XVI.	1917–1933	Botany	3	11	5
XVII.	1917–1920	Zoology	3	10	3
XVIII.	1921	Zoology	4	5	10
XIX.	1924–1925	Zoology	3	7	3
XX.	1924–1926	Zoology	2	12	3
XXI.	1925–1927	Zoology .. ..(excl. Part 1)	1	16	0
XXII.	1925–1928	Palaeontology	2	0	3
XXIII.	1925–1926	Zoology	1	15	5
XXIV.	1929–1938	Anthropology and Ethnology .. ..(excl. Part 2)	2	9	10
XXV.	1927–1928	Zoology	1	19	0
XXVI.	1928	Zoology	1	10	0
XXVII.	1929	Anthropology	1	10	0
XXVIII.	1929–1932	Palaeontology	2	12	3
XXIX.	1929–1931	Zoology	2	8	0
XXX.	1931–1935	Zoology	3	13	10
INDEX of papers, authors, and subjects, published in Vols. I-XXX.. ..			0	1	6
XXXI.	1934–1950	Palaeontology .. .. (Part 4 only)	0	14	0
XXXII.	1935–1940	Zoology	3	3	7
XXXIII.	1939	Zoology	2	2	0
XXXIV.	1938	Zoology	2	8	0
XXXV.	1956	Zoology	6	0	0
XXXVI.	1942–1948	Zoology	2	11	0
XXXVII.	1947–1952	Archaeology	1	16	0
XXXVIII.	1950	Zoology	3	15	0
XXXIX.	1952	Zoology	2	14	6
XL.	1952–1956	Botany .. .. (excl. Index)	1	6	6
XLI.	1952–1955	Zoology	4	0	0
XLII.	1953–1956	Palaeontology	3	7	6
XLIII	1955–	Zoology .. Part 1 £1 0*s.* 0*d.* Part 2	0	5	0

Copies may be obtained from—

The LIBRARIAN, South African Museum, Cape Town.

ANNALS

OF THE

SOUTH AFRICAN MUSEUM

VOLUME XLIII

PART IV, *containing:—*

6. *The Hydrozoa of False Bay, South Africa.* By N. A. H. MILLARD, PH.D., Zoology Department, University of Cape Town. (With fifteen text-figures.)

ISSUED JANUARY 1957 *PRICE* 6*s.*

PRINTED FOR THE
TRUSTEES OF THE SOUTH AFRICAN MUSEUM
BY THE RUSTICA PRESS (PTY.) LIMITED, COURT ROAD, WYNBERG, CAPE

6. *The Hydrozoa of False Bay, South Africa.* By N. A. H. MILLARD, PH.D., Zoology Department, University of Cape Town. (With fifteen text-figures.)

SUMMARY

This paper records a total of sixty-five species of Hydrozoa from False Bay. Of these seven are new records from South Africa, and eight are new species. The latter include *Hydractinia canalifera*, *Eudendrium deciduum*, *Campanularia morgansi*, *Lovenella chiquitita*, *Hebella furax*, *Synthecium hians*, *Sertularella capensis* and *Sertularella falsa*.

INTRODUCTION

The literature on South African hydroids is extremely scattered, most of it in reports on expeditions and museum collections in various parts of the world. Of the early authors, only one, Professor E. Warren, was actually living in the country with free access to the shore and the hydroids in their living condition. It is not surprising, therefore, that a very large proportion of the species, and particularly the more inconspicuous ones, should have escaped notice, and that the existing records should be scattered and incomplete.

Of the early workers the main contributors were Busk (1851), Kirchenpauer (1864, 1872, 1876 and 1884), Allman (1876, 1886 and the Challenger Reports of 1883 and 1888), Marktanner-Turneretscher (1890), Warren (1908 and other papers), Jäderholm (1903, 1917 and 1923), Ritchie (1907a and 1909: Scottish National Antarctic Expedition), Vanhöffen (1910: Deutschen Südpolar-Expedition), Broch (1914: Fauna of West Africa), and Stechow (several papers including the reports of the Deutschen Tiefsee-Expedition). In 1925 Stechow published a check-list of the hydroids reported from South Africa up to that date. This included 153 species, of which 56 were collected by the Valdivia.

Since that date Manton (1940) has described one new species, Ewer (1953) one, and Millard (1955) three. Vervoort (1946a) has recorded eleven species (none of them new) from the Union.

This paper represents the first of what is hoped to be a comprehensive series describing the hydroids of South Africa. It is proposed for convenience to describe the species of different sections of the coast separately, and False Bay has been chosen as a start because of the very large collection which we possess from that area. The material has accumulated from several different sources.

In the first place there is material collected by the old Government survey vessel, the s.s. *Pieter Faure*, at the beginning of the century. This material was submitted to the author for identification by the South African Museum and is referred to by the reference letters PF. Its preservation is not all that might

be desired, but most of the Calyptoblast species can be identified on their skeletal parts.

Secondly, there is a small amount of material collected by Professor T. A. Stephenson and his colleagues in their ecological survey of the coast, and lodged in the Zoology Department of the University of Cape Town. This was all collected in the littoral area at St. James, and is referred to by the reference letter F.

Lastly, the great bulk of the material was collected during the last ten years by members of the Zoology Department working under Professor J. H. O. Day. The littoral material is referred to by the reference letters CP, and the sublittoral material by the letters FB and FAL. The sublittoral material was collected by dredging and by diving with a frogman's outfit. The latter is entirely the result of the enthusiastic work of Mr. J. C. Morgans, who has been conducting a survey of the bottom fauna, and whose results will be published shortly.

The author is indebted to the members of the Zoology Department for their co-operation and help in collecting specimens, and to the Royal Scottish Museum, Edinburgh, and the Zoologische Sammlung des Bayerischen Staates, Munich, for the loan of valuable type material.

Financial aid includes grants from the Staff Research Fund of the University of Cape Town for the purchase of microscope lamps and drawing apparatus, while grants awarded by the C.S.I.R. and the Carnegie Corporation have made possible the purchase of a van and dredging equipment used in the various expeditions. The cost of publication was partly defrayed by a special grant from the publications fund of the University of Cape Town.

Station List

	Date	Position	Depth	Bottom
*PF 337	27/9/98	34°13′S/18°33′E	57 m.	Sand
PF 351	28/9/98	34°19′S/18°31′E (off Buffel's Bay)	58–62 m.	
PF 396	6/10/98	Off Buffel's Bay		
PF 405	8/10/98	Off Buffel's Bay		
PF 5013	8/6/00	34°14′S/18°30′ E (off Miller's Point)	42 m.	Rock
PF 15608	8/10/02	34°25′S/18°35′ E (Rocky Bank)	33 m.	Rock
PF 15675	9/10/02	34°28′S/18°32′E	73 m.	Rock
PF 16287	9/12/02	34°20′S/18°32′E	59 m.	Sand
PF 18232	11/11/03	34°27′S/18°45′E	110 m.	Green mud
PF 18293	7/12/03	34°5·5′S/18°39′E (off Swartklip)	15–18 m.	Rock
CP 15–16	1/5/38	Froggy Pond		
CP 18	30/4/38	Clovelly		
CP 19–20	4/4/38	St. James		
CP 224	29/10/32	St. James		

* The *Pieter Faure* stations have been converted from the compass bearings given in the records, and are given to the nearest minute.

	Date	Position	Depth	Bottom
CP 258	–/4/44	St. James		
CP 259	22/3/47	St. James		
CP 324	22/5/48	St. James		
CP 326	30/12/48	Strandfontein		
CP 332	23/8/49	Clovelly		
CP 333–334	25/8/49	Dalebrook		
CP 356	23/2/51	Buffel's Bay		
CP 377, 380	31/3/53	St. James		
CP 392	27/9/54	Oatland Point		
CP 410	28/9/54	Froggy Pond		
CP 415	29/9/54	Froggy Pond		
CP 426	12/10/54	Oatland Point		
FB 101	8/7/46	34°9′S/18°28′E (off Fish Hoek)	22 m.	Sand
FB 102	8/9/46	34°8·5S/18°27·5′E (off Fish Hoek)	13 m.	?Shell and stones
FB 103	24/11/46	34°8·5′S/18°27·5′E (off Fish Hoek)	15 m.	Shell and sand
FB 104	8/7/46	34°9′S/18°28′E (off Fish Hoek)	22 m.	Sand
FB 105	24/11/46	34°8·5′S/18°27·5′E (off Fish Hoek)	15 m.	Shell and sand
FB 106	8/9/46	34°8·5′S/18°27·5′E (off Fish Hoek)	13 m.	?Shell and stones
FB 107–110	24/11/46	34°8·5′S/18°27·5′E (off Fish Hoek)	15 m.	Shell and sand
FB 111	8/9/46	34°8·5′S/18°27·5′E (off Fish Hoek)	13 m.	?Shell and stones
FB 112	24/11/46	34°8·5′S/18°27·5′E (off Fish Hoek)	15 m.	Shell and sand
FB 113	8/7/46	34°9′S/18°28′E (off Fish Hoek)	22 m.	Sand
FB 114	22/2/47	34°7·5′S/18°31′E (off Muizenberg)	27–28 m.	Rock
FB 115	22/2/47	34°8′S/18°31·5′E (off Muizenberg)	27–28 m.	Sand
FB 116	22/2/47	34°7·7′S/18°31·5′E (off Muizenberg)	23–24 m.	Sand
FB 117	22/2/47	34°7·5′S/18°29·2′E (off Muizenberg)	19–20 m.	Sand
FB 119	21/4/47	34°8·5′S/18°34·5′E (near Seal Is.)	27 m.	Rock
FB 120–121	18/6/47		23–27 m.	Sand and shell
FB 122	28/4/47	34°10′S/18°27·8′E (off Glencairn)	24 m.	Sand
FB 123	28/4/47	34°9·5′S/18°27′E (off Glencairn)	15–19 m.	Sand
FB 126	20/8/47	?Off Strandfontein		
FB 127	26/9/48	34°8′S/18°29·6′E (off Kalk Bay)	18 m.	Sand
FB 128	26/9/48			
FB 129	26/9/48	34°7·1′S/18°29·1′E (off Muizenberg)	19 m.	Rock, shell and sand
FB 130	6/8/47	34°6·9′S/18°30′E (off Muizenberg)	17·5 m.	Sand
FB 131	13/12/49	34°9′S/18°26·7′E (off Glencairn)	5–8 m.	
FB 132	9/3/50	34°8·5′S/18°27′E (off Fish Hoek)	14 m.	Sand
FB 133	18/3/50	34°11′S/18°27·3′E (off Simonstown)	25 m.	Sand
FB 134	5/4/50	34°8·9′S/18°27·4′E (off Glencairn)	15 m.	Sand
FB 136	27/8/51	34°9·6′S/18°26·6′E (off Glencairn)	17 m.	Rock
FB 137	27/8/51	34°10·2′S/18°26·2′E (off Glencairn)	14 m.	Shell and sand
FB 138	27/8/51	34°10·1′S/18°26·1′E (off Glencairn)	9 m.	Sand
FB 139	27/8/51	34°10·0′S/18°26·1′E (off Glencairn)	10 m.	
FB 140	27/8/51	34°9·3′S/18°26·4′E (off Glencairn)	11 m.	Rock

	Date	Position	Depth	Bottom
FB 141	20/9/50	34°7·5′S/18°29′E (off St. James)	14·5 m.	?Sand and rock
FB 142	20/9/50	34°7·5′S/18°29′E (off St. James)	16·5 m.	Sand and stones
FB 143	27/8/51	Off Glencairn	8 m.	Rock
FB 144	29/4/48	34°10·2′S/18°27·8′E (Roman Rock)	26–29 m.	Sand
FB 145	29/4/48	34°9·2′S/18°26·8′E (off Glencairn)	20–23 m.	Sand and shell
FB 146	26/9/48	34°8·5′S/18°30′E (off Muizenberg)	24 m.	Shell and sand
FB 147	26/9/48	34°7·5′S/18°29·5′E (off Muizenberg)	14 m.	Sand
FAL 6, 7 and 13	22/2/52	34°8·2′S/18°35·3′E (near Seal Is.)	24 m.	Rock
FAL 15	5/3/52	34°12·5′S/18°28′E (SE of Oatland Point)	8–9 m.	Sand and rock
FAL 20, 23	5/3/52	34°13′S/18°28′E (off Spaniard Rock)	11–12 m.	Shell and rock
FAL 26	5/3/52	34°13′S/18°29′E (off Miller's Point)	15–21 m.	?Sand and shell
FAL 34	18/6/52	34°5′S/18°44′E (off Kromhout Rock)	7 m.	Sand and rock
FAL 42	25/6/52	34°9·6′S/18°49·2′E (off Gordon's Bay)	21–22 m.	Sand and rock
FAL 51–52	25/6/52	34°9·3′S/18°49·6′E to 34°9′S/18°50·1′ E (off Gordon's Bay)	18 m.	Rock and sand
FAL 56	25/6/52	34°9·4′S/18°50·8′E to 34°9·5′S/18° 50·9′E (off Gordon's Bay)	8 m.	Rock
FAL 58	25/6/52	34°9·4′S/18°50·4′E (off Gordon's Bay)	12 m.	Sand and rock
FAL 60	29/7/52	34°17·8′S/18°49·3′E (off Rooi Els)	7–10·5 m.	Sand
FAL 61–62	29/7/52	34°17·5′S/18°49·2′E (off Rooi Els)	22 m.	Sand
FAL 64	29/7/52	34°17·3′S/18°48·7′ E (off Rooi Els)	37–38 m.	Shell and ?sand
FAL 66	29/7/52	34°17·2′S/18°49·4′E (north of Rooi Els)	16–19 m.	Rock
FAL 78, 82	19/8/52	34°16·5′S/18°49·5′E (north of Rooi Els)	14–17 m.	Rock
FAL 95	17/9/52	34°10·6′S/18°47·3′E (off Gordon's Bay)	36 m.	Rock and sand
FAL 108	23/1/53	34°9·3′S/18°51′E (Gordon's Bay)	8–12 m.	Rock and sand
FAL 115	12/2/53	34°11′S/18°25·6′E (Simon's Bay)	3–5 m.	Shell and sand
FAL 123	17/2/53	34°10′S/18°26′E (off Glencairn)	7 m.	Rock and sand
FAL 125	17/2/53	34°10′S/18°26′E (off Glencairn)	2–4 m.	Rock
FAL 132	27/2/53	34°12·5′S/18°28′E (Oatland Point)	0–2 m.	Rock
FAL 137	4/3/53	34°9·8′S/18°51·5′E (Gordon's Bay Pier)	0–4 m.	Rock
FAL 141	9/3/53	34°12·5′S/18°28′E (Oatland Point)	0–5 m.	Rock
FAL 148	12/3/53	34°12·5′S/18°28′E (Oatland Point)	5·5–6·5 m.	Stones, rock and sand
FAL 153, 154, 159	21/4/53	34°12·5′S/18°28′E (Oatland Point)	0–3 m.	Rock

	Date	Position	Depth	Bottom
FAL 160	23/5/53	34°12·5′S/18°28′E (Oatland Point)	0–3 m.	Rock
FAL 165, 167	10/6/53	34°12·5′S/18°28′E (Oatland Point)	2–4 m.	Rock
FAL 169, 174	10/6/53	34°12·5′S/18°28′E (Oatland Point)	4–6·5 m.	Rock
FAL 176	10/6/53	34°12·5′S/18°28′E (Oatland Point)	0–2 m.	Rock
FAL 177	9/8/53	34°12·5′S/18°28′E (Oatland Point)		
FAL 183	11/9/53	34°22·1′S/18°35·2′E (north of Rocky Bank)	73 m.	Shell and sand
FAL 186	10/9/53	34°12·8′S/18°36·5′E	46 m.	Shell and sand
FAL 205	10/9/53	34°17·6′S/18°39·2′E	62 m.	Shell and ?sand
FAL 207	10/9/53	34°9·9′S/18°42·4′E	36·5 m.	Rock and sand
FAL 209	10/9/53	34°6·8′S/18°40·3′E (off Swartklip)	29 m.	Shell and sand
FAL 211	9/9/53	34°7·1′S/18°35·6′E (off Strand-fontein)	22 m.	Rock, sand and shell
FAL 214	10/9/53	34°12·4′S/18°43·5′E	42 m.	Rock
FAL 217	9/9/53	34°7·0′S/18°32·5′E (NW of Seal Is.)	18 m.	Rock, sand and shell
FAL 222–223	9/9/53	34°13·9′S/18°31·6′E (off Miller's Point)	40 m.	Sand and shell
FAL 230	9/9/53	34°17·3′S/18°31·4′E (off Buffel's Bay)	49 m.	
FAL 238	10/9/53	34°20·6′S/18°39·4′E	82 m.	?Shell, sand and green mud
FAL 258	21/11/53	34°12·5′S/18°28′E (Oatland Point)		Shell and sand
FAL 262	21/11/53	34°11·6′S/18°27·3′E (Noah's Ark)	11–14 m.	Rock
FAL 268	18/9/54	34°10·9′S/18°27·2′E (Roman Rock)	15–18 m.	Rock
FAL 274	21/9/54	34°10·9′S/18°27·2′E (Roman Rock)	14–17 m.	Rock
FAL 279, 282	23/9/54	34°10·9′S/18°27·2′E (Roman Rock)	12–14 m.	Rock
FAL 288	15/10/97	34°9·6′S/18°49·8′E (off Gordon's Bay)	18 m.	?Rock
FAL 289–290	–/9/97		40 m.	
FAL 291	24/3/98			
FAL 292	21/10/03	Kalk Bay		
FAL 311	11/4/55	34°12·5′S/18°28′E (Oatland Point)	0–2 m.	Rock

List of Species

Gymnoblastea

Corynidae

Coryne sp.

Tubulariidae

Tubularia solitaria Warren
Tubularia sp.

Bougainvilliidae

Hydractinia altispina Millard
Hydractinia canalifera n. sp.
Hydractinia carnea (M. Sars)
Hydractinia sp.
Leuckartiara octona (Fleming)
Hydrocorella africana Stechow

Eudendriidae

Eudendrium ?antarcticum Stechow
Eudendrium deciduum n. sp.

Myriothelidae

Myriothela capensis Manton

Calyptoblastea

Haleciidae

Hydrodendron caciniformis (Ritchie)
Halecium beanii (Johnston)
Halecium dichotomum Allman
Halecium parvulum Bale
Halecium tenellum Hincks

Campanulariidae

Campanularia integra MacGillivray
Campanularia morgansi n. sp.
Clytia gracilis (M. Sars)
(*Clytia raridentata* (Hincks))
Obelia dichotoma (Linnaeus)
Obelia geniculata (Linnaeus)

Campanulinidae

Lovenella chiquitita n. sp.

Lafoeidae

Hebella furax n. sp
Hebella scandens (Bale)
Scandia mutabilis (Ritchie)
Reticularia serpens (Hassall)
Zygophylax cornucopia Millard

Syntheciidae

Synthecium ?elegans Allman
Synthecium hians n. sp.

Sertulariidae

Dictyocladium coactum Stechow
Salacia articulata (Pallas)
Sertularella africana Stechow
Sertularella abuscula (Lamouroux)
Sertularella capensis n. sp.
Sertularella falsa n. sp.
Sertularella flabellum (Allman)
Sertularella fusiformis (Hincks)
Sertularella goliathus Stechow
Sertularella mediterranea Hartlaub
Sertularella megista Stechow
Sertularella polyzonias (Linnaeus)
Sertularella xantha Stechow
Symplectoscyphus macrogonus (Trebilcock)
Amphisbetia bidens (Bale)
Amphisbetia minima (Thompson)
Amphisbetia operculata (Linnaeus)
Sertularia distans (Lamouroux)
Sertularia marginata (Kirchenpauer)

Plumulariidae

Antennella africana Broch
Halopteris constricta Totton
Halopteris valdiviae (Stechow)
Paragattya intermedia Warren
Plumularia lagenifera Allman
Plumularia pulchella Bale
Plumularia setacea (Ellis and Solander)
Plumularia spinulosa Bale
Kirchenpaueria pinnata (Linnaeus)
Pycnotheca mirabilis (Allman)
Nemertesia cymodocea (Busk)
Nemertesia ramosa Lamouroux
Antennopsis scotiae Ritchie
Aglaophenia pluma (Linnaeus)
Thecocarpus giardi Billard.
Lytocarpus filamentosus (Lamarck)

Family **Corynidae**

Coryne sp.

Records. FAL 311 T. CP 326 F.

Description. Several branching stems reaching 0·8 cm. in length, one with young gonophores, but too small to determine structure. Stem smooth or irregularly corrugated in parts, pedicels of hydranths annulated at base. Hydranths approximately 1 mm. in length.

Remarks. There is nothing in the appearance of the colony to exclude it from *Coryne eximia* Allman, but in the absence of mature gonophores the specimens cannot be finally identified.

Family **Tubulariidae**

Tubularia solitaria Warren 1906a.

Tubularia solitaria Warren 1906a; p. 83; Pl. X and XI.

Records. F 231 (recorded by Eyre 1939). CP 326 D.

Description. Gonophores present in December.

Tubularia sp.

Records. CP 326 E. FAL 153 X.

Description. A few small specimens with well-developed perisarc, and hydranths without gonophores.

Remarks. Due to the paucity of the material and the absence of gonophores the identification cannot be completed.

Family: **Bougainvilliidae**

Hydractinia altispina Millard 1955

Hydractinia altispina Millard 1955; p. 215; fig. 1.

Records. F 274. CP 258, 377. FAL 7 Z. (Recorded by Millard 1955.)

Hydractinia canalifera n. sp.

Fig. 1

Type. Holotype CP 332 in University of Cape Town.

Description. A single colony growing on weed in the littoral area. Hydrorhiza forming an intimately anastomosing feltwork, encrusted in centre of colony, but not at periphery.

Gastrozooids large, reaching 2–3 mm. in height (preserved), with 10–14 tentacles in a single whorl. Manubrium conical when contracted, but capable of great expansion and even of turning completely inside-out.

No spines. No spiral zooids, but a very few tentacular filaments scattered amongst the gastrozooids.

Gonozooids smaller than gastrozooids, each with a mouth and a single whorl of 6–9 short tentacles, bearing a cluster of 4 or 5 sporosacs on the upper half

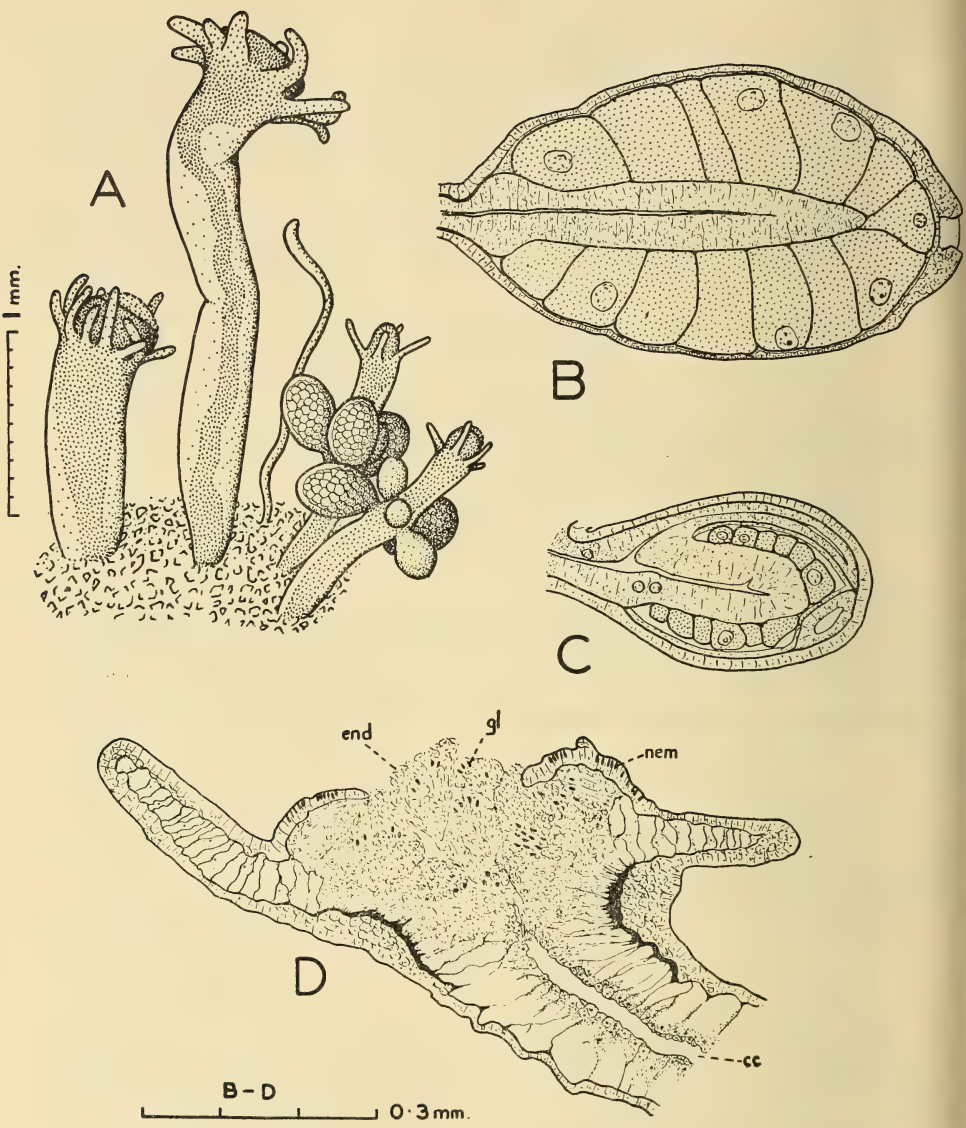

FIG. 1. *Hydractinia canalifera* n. sp. from the holotype.

A. Portion of a colony, showing 2 gastrozooids, a tentacular filament, and 2 female gonozooids bearing sporosacs. B. Longitudinal section through mature female sporosac. Radial canals not visible. C. Longitudinal section through young female sporosac, passing through one radial canal and the circular canal. D. Longitudinal section through gastrozooid, showing central canal (*cc*) of stem, and endodermal plug (*end*) blocking the mouth. *gl*, gland cells; *nem*, nematocysts.

of the stem. Female sporosacs only present, ovoid, containing many eggs (estimated as well over 50). Radial canals and circular canal present in young sporosacs, though not visible in older ones. Manubrium with a very restricted cavity. No vestige of tentacles.

Detailed Anatomy. The structure of the zooids is interesting and unusual. Under the dissecting microscope and in whole mounts a distinct central tube can be seen passing up the stem to expand into a mass of solid tissue within the tentacle-ring and completely blocking the mouth. Sections reveal that the narrow central canal is formed by the massing of the cytoplasm in the inner ends of enormously elongated endoderm cells. The outer ends of the cells resting on the mesogloea are swollen and vacuolated, and tend to run together to form a system of open spaces surrounding the central canal.

Near the top of the stem the central canal merges with a solid mass of small endoderm cells which fills all the cavity within the tentacle-ring. Large darkly staining gland cells are visible in the mass. Sometimes a series of crevices puts the central canal or even the outer space into communication with the exterior, but in most cases there is no communication whatever. In a few zooids the central plug of endoderm is actually extruded beyond the level of the manubrium, and in cases where the manubrium has turned inside-out, a large area of endoderm is exposed to the exterior.

Measurements (preserved material)

Gastrozooids reaching 3·16 mm. to origin of tentacles. Gonozooids reaching a maximum height of 1·25 mm. to origin of tentacles.

Female sporosac, maximum length	0·76 mm.
maximum diameter	0·53 mm.

Remarks. H. canalifera is very close to *H. kaffraria* Millard 1955, but can be distinguished by its larger and more robust zooids, and particularly by the internal modifications of the endoderm.

The only other hydroid known to the author in which the digestive cavity is blocked by endoderm is *Eudendrium angustum* Warren 1908, in which food matter is directly ingested by the endoderm cells. It is probable that a similar method of feeding is employed by *H. canalifera*, and the extrusion of the endoderm and eversion of the manubrium suggests that secretions may also be poured over the food outside the body.

Hydractinia carnea (M. Sars) 1846

Podocoryne carnea Hincks 1868; p. 29; Pl. V.

?*Hydractinia parvispina* Vanhöffen 1910, p. 291.

Hydractinia carnea Vervoort 1946, p. 126, fig. 49.

Records. FB 108, 121 B. FAL 64 W, 205 C, 209 D, 238 B.

Description. Colonies fairly common in dredgings on shells of *Hinia speciosa* (Adams). Hydrorhiza an open meshwork in younger parts of colony, completely encrusted in older parts, spines present only in fully encrusted areas.

Ripe gonophores, however, may be present in areas which are not fully encrusted.

The development of the medusoid individuals at the time of liberation varies considerably and does not seem to depend on the season. I have seen a gonozooid bearing two gonophores, one of which was a small but perfectly developed medusa with 4 tentacles and no sexual products, and the other much larger and filled with spermatogenic cells, yet with the tentacles undeveloped. Female medusoids are often packed with eggs at the time of liberation, the number varying from 27 to 40. Gonophores present in June, July, September and November.

Remarks. It is highly probable that the material reported from Simonstown as *H. parvispina* on *Nassa* by Vanhöffen is the same species with precociously developed sexual products.

Hydractinia sp.

Records. FAL 183 N.

Description. Hydrorhiza encrusted. Spines smooth, long and hollow, reaching a maximum length of 1·5 mm. Gastrozooid about 4 mm. long. Gonozooids smaller, tentacular. Gonophores in the form of fixed sporosacs, no radial canals visible. Smaller ones female, containing tightly packed eggs. Larger ones male or hermaphrodite, the latter containing a few scattered eggs packed amongst masses of spermatogenic material.

Remarks. The material is in a very poor state of preservation, and the nature of the gastrozooids and gonozooids cannot be determined. The species appears to be closely related to *Hydractinia altispina* Millard 1955, although hydranths and spines are somewhat longer. The sporosacs are better preserved than the hydranths, and appear to be unique in their hermaphroditic nature.

Leuckartiara octona (Fleming) 1823

Eudendrium repens Wright 1858.

Leuckartiara octona Rees 1938, p. 12 (synonymy), figs. 3–5.

Records. FB 121 C, 136 C, 138 A, all on *Bullia annulata* (Lamarck). FAL 60 C, 61 B, 115 E, 209 C, on *Bullia annulata* (Lamarck); FAL 238 C on *Nassarius circumtectus*.

Description. Colonies fairly common on the shells of certain gastropods. The form of the colony is very similar to that described by Rees 1938 from the shell of a *Turritella* inhabited by a hermit crab.

On the 'under' side of the shell the stems are low and the hydranths small, the whole colony not exceeding 1 mm. in height. No gonophores are present in this region and often no hydranths, the shell being covered only by the reticular hydrorhiza.

On the 'upper' side of the shell and round the tip of the spire the colony is much better developed and reaches a height of 3–5 mm. The stems are long

and occasionally branched, and bear numerous gonophores. Only once was a gonophore seen to arise from the hydrorhiza.

Perisarc annulated or coarsely wrinkled at base of stem, widening distally and continued over hydranth to bases of tentacles where it ends abruptly. Hydranths with 6–12 tentacles, usually held alternately elevated and depressed.

Gonophores with short annulated pedicels, completely invested by transparent perisarc. Medusae with 2 long tentacles when ready to leave. Gonophores present from June to September.

Measurements (in mm., preserved material)

Hydrorhiza, diameter	0·04–0·07
Stem, diameter at base	0·045–0·07
Pseudohydrotheca, length	0·22–0·37
maximum diameter	0·19–0·38
Hydranth, length to tip of manubrium	0·30–0·51
Gonophore, length	0·30–0·60
diameter	0·18–0·45

Hydrocorella africana Stechow 1921c

Hydrocorella africana Stechow 1925, p. 409.

Records. FB 114 B, 115 C, 122 B, 123 B, 125 B, 136 D, 137 B, 143 A, 144, 145.

Description. Fertile colonies growing on empty gastropod shells. Gonophores borne in clusters on gonozooids which are smaller than the gastrozooids and possess about 6 rudimentary tentacles. Gonophores present in February.

Family: **Eudendriidae**

Eudendrium ?antarcticum Stechow 1921a

Eudendrium antarcticum Stechow 1925, p. 415, fig. 5.

Records. FAL 288 H.

Description. Hydrorhiza creeping on other hydroids. Stem unbranched or sparingly branched, reaching a maximum height of 3 mm.; annulated at base, on origins of branches and occasionally for short distances in other regions. Perisarc terminating abruptly below hydranth. Hydranth with about 20 tentacles (19–23 in 8 counts) and a distinct annular groove near base.

Male gonophores borne in clusters on completely atrophied hydranths which arise from the stem or, more frequently, direct from the hydrorhiza. Pedicel annulated. Gonophore one-chambered, with a distinct tubercle at distal end. Present in October. Female gonophores absent.

Measurements (in mm., preserved)

Stem, diameter	0·055–0·075
Hydranth, length to tip of manubrium	0·20–0·30
diameter at tentacle roots	0·11–0·16
Gonophores, male, length	0·15–0·22